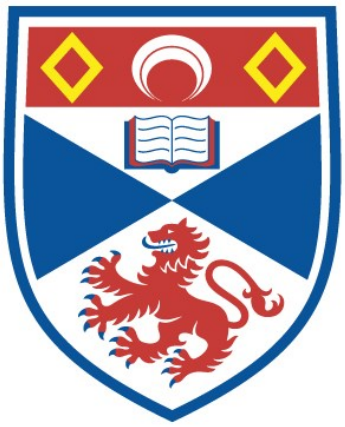
THE COMPARITIVE ANATOMY OF THE INTERVERTEBRAL JOINTS

Kamal Kumar Banerji

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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THE COMPARATIVE ANATOMY OF THE INTERVERTEBRAL JOINTS

BY

KAMAL KUMAR BANERJI

A THESIS

PRESENTED FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

OF

THE UNIVERSITY OF ST. ANDREWS

MS 2023

DECLARATION

I hereby declare that the following Thesis is based on the results of experiments carried out by me, that the Thesis is my own composition, and that it has not previously been presented for a Higher Degree.

The Research was carried out in the Department of Anatomy, Bute Medical Buildings, University of St. Andrews.

(Kamal Kumar Banerji)

CERTIFICATE

I certify that Kamal Kumar Banerji has spent nine terms at Research work in the Department of Anatomy under my direction, that he has fulfilled the conditions of Ordinance No. 16 (St. Andrews) and that he is qualified to submit the accompanying Thesis in application for the degree of Ph.D.

Professor of Anatomy,
St. Salvator's College,
University of St. Andrews.
1st February, 1957.

CAREER

In 1945, I graduated M.B., B.S., from the University of Calcutta, India. After completing Residential Hospital training for 2 years and 9 months, I worked as a Senior Demonstrator and Assistant Professor of Anatomy for 6 years in the N. R. Sircar Medical College, as well as held the additional teaching post of Demonstrator in Dental Anatomy at Calcutta Dental College, of the same University.

On September, 1954, I commenced the Research on 'The Comparative Anatomy of the Intervertebral Joints' under the supervision of Professor R. Walmsley, and have completed the work which forms the subject of this Thesis.

(Kamal Kumar Banerji)

CONTENTS

LIST OF ABBREVIATIONS

USED IN TEXT-FIGURE AND PLATE

Af.	Artefact
An. F.	Annulus Fibrosus
Ao.	Aorta
Art. Cart.	Articular cartilage
B.	Axial band
Cap. Lig.	Capsular ligament
Cart. En.	Cartilage - envelope
Cen. Lig.	Central ligament
Ch. Epi.	Chordal epithelium
D.L. Lig.	Dorsal longitudinal ligament
El. Ex.	Elastica externa
El. Int.	Elastica interna
Epi.	Epiphysis
H.L.	Homogeneous layer
Hae.	Haemapophysis
Hy.	Hypapophysis
Iv. D.	Intervertebral disk
Iv. Lig.	Intervertebral ligament
Iv. M.	Intervertebral meniscus
Iv. R.	Intervertebral region

J.C./

J.C.	Joint cavity
M.M.	Mucoid material
N.P.	Nucleus pulposus
N.S.	Notochordal sheaths
Nch.	Notochord
Nch. C.	Notchordal cells
Nch. V.	Notochordal vestige
S.	Space
Sp. C.	Spinal cord
Sy. F.	Synovial fold
Sy. M.	Synovial membrane
T. F.	Tail-fin
Ur.	Urostyle
V.	Vacuole
V.B.	Vertebral body
V.L. Lig.	Ventral longitudinal ligament

INTRODUCTION

Introduction:

The study of the intervertebral joints in the vertebrate group, except human, has received very little attention. Indeed, the whole problem has been mostly neglected, and no effort has yet been made to compare the intervertebral joints of the mammalian vertebral column with those of the submammalian forms. A thorough study, of their structure and function, will help to give a proper understanding of the principles underlying the organisation of the joints of the column in man.

The manner in which the articulations of the vertebral bodies, in different vertebrate animals, have become variously modified, in relation to diverse function in the process of evolution, has attracted the writer's attention to select this present investigation. Relatively few workers have pursued a proper comparative study of the intervertebral joints, in order to elucidate the remarkable similarities between them, although they are in no way absolutely homologous. Variations on the general scheme are indeed presented by the different genera within each class but, within the limits imposed by specialisation and modification, all the intervertebral joints from fish to mammal conform to an independent pattern of development and growth. The most marked modifications are naturally presented/

presented with the change from aquatic to land life, when entirely new demands were imposed upon the animal body; in this evolutionary process the entire vertebral column became adaptively changed. This study is not only intended to extend our knowledge of the intervertebral joints in general, but also to establish a functional correlation with structure and growth, which may serve as a basis for studying the evolutionary changes in them.

The present investigation is entirely restricted to the study of the joints between the bodies of the vertebrae in different vertebrate animals; it presents the data thus obtained, as well as an analysis and comparison with previously published accounts. It is obvious that the work will not be complete unless the joints between the atlas and the axis, and those between the neural arches have been thoroughly investigated.

The voluminous literature, covering the development of the vertebral column of different vertebrate forms, will not be reviewed here, but references to some of these workers will be found in this work, where necessary. Flower (1885) and Owen (1886) have published a considerable amount of literature on the variations in form and number of the vertebrae in different vertebrate animals. Carlier (1890) has given a detailed account of the fibre arrangement of/

of the intervertebral disk in adult sheep. Gagenbaur (1898) and Gadow (1933) have attempted to compare the structures of the intervertebral region in different higher vertebrates. Rockwell, Evans and Pheasant (1938) have given a comprehensive idea of the evolution of the vertebral column from a functional view point.

As there is a marked similarity between the basic structure of the intervertebral joints in mammals and in man, the relevant literatures on the latter will be reviewed and discussed. A detailed study of the human intervertebral disk has been carried out by Virchow (1857), Luschka (1858), Kölliker (1867), Robin (1868), Dursy (1869), Löwe (1879), Beadle (1931), Keys and Compere (1932), Coventry, Ghormley and Kernohan (1945, parts I & II), Peacock (1951, 1952), and Walmsley (1953).

An attempt has also been made in this paper, to give an account of the form, structure and fate of the notochord in pre- and post-hatched Birds, since this structure is intimately related to their intervertebral joints. Piiper's (1928) remarks on the notochordal changes in embryonic birds will be referred to and discussed.

MATERIAL AND METHODS

Material and Methods:

The material used for this investigation consisted of five salmo salar (Pisces), five Rana temporaria temporaria (Amphibia), six Lacerta viridis (Reptilia), forty-five Gallus domesticus (Aves) and sixteen Mus Norvegicus albinus (Mammalia). All the material was adult only except the bird and the mammal. The specimens of the bird varied in age from one day old chicks to two year old hens, and those of the mammals from one day to two year old rats. Fifteen chick embryos, of three, ten, fifteen and eighteen days incubation, were also examined for a comprehensive study of the notochord. The above series of animals were selected for this research because they were easily obtained.

The age and weight of each specimen was recorded, and all the animals, except the chick embryos were killed by coal gas. The tissues were fixed by injection with 10% neutral formol-saline (NaCl - 0.85% for mammals, 0.75% for birds, 0.65% for reptiles, amphibia and fishes), and were kept in this solition for at least 7 to 10 days. The chick embryos were fixed in Bouin's and Zenker's fluids, both these fixatives gave good results.

The vertebral column of each specimen was dissected out/

out. The nature of the curvatures and the length of the whole column and its different regions were noted. The intervertebral joints were dissected and examined under a binocular microscope.

All embedding was done in paraffin and serial sections 10 μ thick were cut, sagittally from right to left, and a few coronal and transverse sections were also cut. Every fifth section was taken on albumenised slides, and, in general, these were stained with Ehrlich's Haematoxylin and Eosin; some were treated with Weigert's (elastic tissue) and Krajian's stains, for the demonstration of elastic fibres.

Diagrammatic figures were drawn in order to elucidate the reciprocal relations of different structures. Microphotographs of the sections were also taken at different magnifications.

Remarks:

1. Cutting of serial sections of the embryos was excellent, and the best results were obtained by clearing in methyl salicylate from 90% alcohol and passing the embryos rapidly through cedarwood oil directly into paraffin wax 52° m.p. They were then passed through two or more paraffin/

paraffin baths, and removed from the bath in twenty to twenty-five minutes. A longer period in the bath, a higher temperature and sometimes absolute alcohol for dehydration resulted in excessive fracturing on sectioning.

2. Considerable difficulty was experienced in cutting the sections of adult birds and rats due to the presence of tough and thick fibrous connective tissue.

3. After the removal of paraffin, a considerable number of sections were coated with 1% celloidin in alcohol-ether before proceeding to water; this prevented them from coming away from the slides.

OBSERVATIONS

THE INTERVERTEBRAL JOINTS OF PISCES

Observations:

SUPER-CLASS - Pisces (or Fishes)

CLASS - Osteichthyes or Teleostomi

SUB-CLASS - Actinopterygii

ORDER - Teleostei

SUB-ORDER - Salmonidae

SPECIES - Salmo salar

AGE - 3 years (+)

WEIGHT - 27 gms.

LENGTH OF THE VERTEBRAL COLUMN - 11.3 cm.

LENGTH OF THE TRUNK REGION - 5 cm.

LENGTH OF THE TAIL REGION - 6.3 cm.

The vertebral column of the Salmon (Salmo salar) usually consists of fifty-nine free bony vertebrae. The column is divisible into two regions, a trunk region in which the vertebrae bear movable ribs, and a caudal or tail region in which the vertebrae bear haemal arches.

The/

The joints between the bodies of the vertebrae are fibrous in type or syn-arthrosis. The contiguous vertebral bodies are connected together by bi-convex, fibro-gelatinous intervertebral disks and by ligaments.

Each vertebral body is a short cylinder of bone and as the vertebrae are amphicoelous both the cranial and the caudal surfaces are concave (Fig. 1). The concavities are deep and the central zones are deficient, which allows adjacent intervertebral disks to communicate with one another through canals that lie within the cortical bone of the vertebral bodies. The first few vertebrae have very short bodies but those of the succeeding vertebrae gradually lengthen, until the middle of the caudal region where they again gradually become shorter and shorter as they are traced caudally. The caudal extremity of the vertebral column stops short of the free margin of the caudal fin (Fig. 5). The vertebral segment of the tail is deflected dorsally from the general axis of the column into the tail fin (Fig. 5). The body of the last vertebra is a rod-like structure and is called the urostyle. Through the series of vertebral bodies runs the remnant of the notochord, which is markedly constricted within the bodies but widely dilated in the large inter-

vertebral spaces, in each of which it forms a soft pulpy mass. Thus the remains of the notochord and its sheaths persist as a continuous chain of moniliform appearance throughout the length of the vertebral column. At the caudal end of the tail, however, the notochord extends a little beyond the urostyle, where it is enclosed in a fibrous envelope (Fig. 5).

Intervertebral Disk:

The intervertebral disks are bi-convex, fibro-gelatinous structures that connect the concave surfaces and the margins of the adjoining vertebral bodies (Figs. 1 and 3). Each disk consists of two portions, a peripheral annular portion and a central gelatinous portion. This latter forms the main bulk of the disk.

The peripheral annular portion is in turn composed of two parts namely, an outer homogeneous layer and an inner layer which represents the notochordal sheath. The outer homogeneous stratum which is not more than 10 μ in thickness, bulges out beyond the limits of the margins of the adjoining vertebral bodies (Figs. 3 and 4). Its peripheral surface is intimately attached to a well-defined intervertebral ligament, which extends as a cuff between/

between the adjacent vertebral bodies, but its inner surface is only loosely connected with the notochordal sheath. The same homogeneous outer layer when traced towards a vertebra covers its concave surfaces and in turn can be traced into the central canal which it lines completely.

The notochordal sheath consists of a ring of closely packed concentric fibres with no cells between them. It is divided into two layers, namely a superficial layer of highly refractile substance termed the elastica externa, and a deeper layer of fine fibrils in a homogeneous ground substance, the elastica interna.

The refractile elastica externa consists of compact elastic fibres and is about 7 μ in thickness at the circumference of the disk where it has a similar bulge (Figs. 3 and 4) as that of the outer annular homogeneous layer. In the vertebral region it is followed as a thinner layer, and passes into the canal but the identity is lost before the middle of the canal is reached. The outward bulging of the elastica externa is loosely attached to the annular homogeneous layer superficially, and its deep surface is connected to the elastica interna.

The/

The elastica interna presents a considerable thickness in the circumferential zone of the disk (Figs. 3 and 4); it lies between the elastica externa externally and the chordal epithelium internally and is attached to both of them intimately. It consists of fine collagen fibres arranged in compact irregular lamellae but no cells are apparent between them. In the vertebral region, however, this layer becomes extremely thin and eventually gets lost like the outer homogeneous layer and elastica externa, when traced towards the central canal. The elastica interna, in the young specimens examined, is not so well-marked (Fig. 6) as it is in the adult fish.

The gelatinous portion of the intervertebral disk consists entirely of the remains of the notochordal tissue. Three zones are distinguished from the centre towards the periphery, each gradually merging with the other (Figs. 2 and 3). The internal zone is at the centre of the disk and consists of a thick, broad mass of protoplasmic fibres with a few vacuolated cells of various sizes and shapes. A few cells show nuclei at various stages of degeneration, but in others these are absent. The next zone presents a very loose network of fibres with a few nuclei in its wall. The most superficial zone, on the other hand, consists/

consists of a somewhat denser ground substance with a few nuclei embedded in it, and this zone forms the chordal epithelium (Figs. 3 and 4). The outline of the cells is not clearly distinguished in this zone. The chordal epithelium is thicker in the circumferential zone of the disk, and the nuclei there are so closely united, that they give the appearance of columnar epithelium. In the vertebral region, on the other hand, the epithelium is more sparse near the concave surface and gradually disappears in the vertebra.

From the internal zone of the gelatinous portion, a longitudinal axial band is prolonged both cranially and caudally through the central canal of the adjacent vertebral bodies. Each axial band is formed of compact longitudinal fibres containing a few nuclei, whose cytoplasm is not visible (Figs. 1 and 3).

In the vertebral region the notochord is constricted to a mere thread. A big space is seen to split it into a central portion, which forms the axial band (Fig. 1), and a peripheral portion applied to the wall of the bony cavity.

Intervertebral Ligament:

The/

The entire margins of contiguous vertebral bodies are firmly connected together by a white fibrous inter-vertebral ligament (Figs. 3 and 4). The ligament is thicker and stronger in the two dorso-lateral and two ventro-lateral regions of the joint. Each ligament consists of short arched collagen fibres passing from the margin of one bone to the margin of the other with their convexities outwards (Fig. 4). The fibres are few in number with many young fibroblasts lying between them, and this character is especially noticed in the young specimens examined (Fig. 6). The deep surface of the ligament is attached to the outer annular homogeneous layer of the disk, and superficially it is reinforced by the ventral and dorsal longitudinal ligaments.

The intervertebral ligaments of the first six or seven joints of the trunk region and the terminal three or four joints of the caudal region are thicker and stronger than the others.

Small blood vessels are present ventrally in the substance of the intervertebral ligament, close to its attachment to the bony margins.

Ventral and Dorsal Longitudinal Ligaments:

Two longitudinal ligaments exist, one running along the/

the dorsal and the other along the ventral aspect of the column. They extend from the base of the skull to the urostyle. The dorsal ligament extends laterally as far as the roots of the neural arches, while the ventral ligament extends to the ribs, or haemal arches in the caudal region. In each vertebral region these ligaments are thin and are blended with the periosteum covering the vertebral bodies, but in the intervertebral regions, the ligaments are much thicker. The deep surface of both ventral and dorsal longitudinal ligaments is intimately connected with the intervertebral ligaments described above.

THE INTERVERTEBRAL JOINTS OF AMPHIBIA

Observations:

CLASS - Amphibia

SUB-CLASS - Euamphibia

ORDER - Anura

SPECIES - Frog (Rana temporaria temporaria)

AGE - 3 years (+)

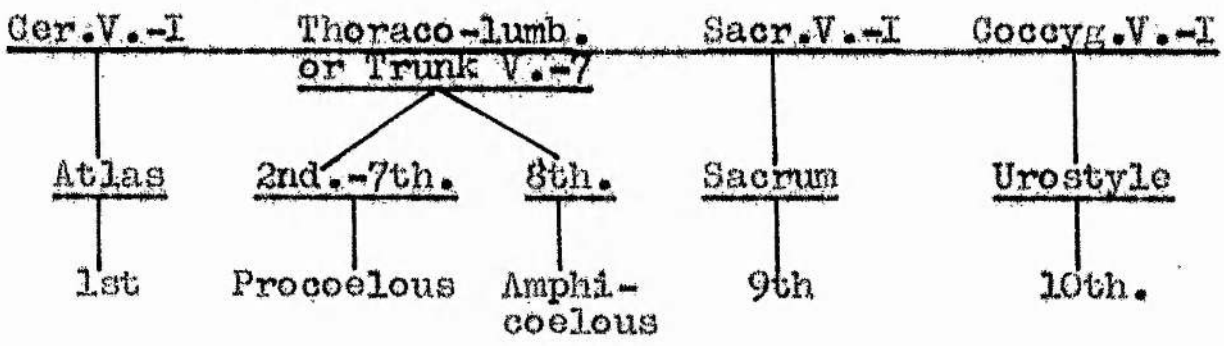
WEIGHT - 17.5 gms.

LENGTH OF THE VERTEBRAL COLUMN - 5 cm.

LENGTH OF THE UROSTYLE - 2.4 cm.

The vertebral column of the adult frog is remarkably short and it consists of ten bony segments, all free; the first nine of these are formed of small ring-like bones, called the vertebrae, and the tenth segment is a long slender rod of bone, the urostyle or os coccygeum. The urostyle forms almost half the total length of the column.

Four regions of the vertebral column may be recognised as follows:



The/

The joints between the bodies of the vertebrae are of the synovial ball and socket type. Moreover, the neural arches of the vertebrae articulate by a series of plane synovial joints.

Although the type of joint between the vertebral bodies is the same throughout the vertebral column of frog, the first, eighth, ninth and tenth vertebrae differ in their form from the others.

The vertebrae from the second to the seventh have a common form and their bodies show similar characters. Each vertebral body is a short cylinder of bone, somewhat flattened dorso-ventrally. The cranial articular surface is deeply concave with its greatest diameter lying transversely, while the caudal articular surface is a rounded convex knob (Fig.7). This form of vertebra is called procoelous. The peripheral margin of the concave articular surface of each vertebral body extends cranially as a thin bony lamina beyond the limit of the articular cartilage which covers it (Figs. 7 and 8). This feature is very characteristic of these vertebrae.

The first and the only cervical vertebra, called the atlas, presents a flat dorso-ventrally compressed vertebral body. Cranially, it articulates by two lateral oval concave facets with the two occipital condyles;/

condyles; caudally, however, the body of the atlas presents a small convex articular surface for the articular cup at the cranial end of the second vertebral body.

The eighth vertebra, smallest of all, is concave on both cranial and caudal surfaces of its body, and is therefore amphicoelous in form (Fig.8). Each concave articular end receives the convex articular ball of the vertebral bodies cranial and caudal to it.

The ninth vertebra, or the sacrum, differs from the other vertebrae in having«convex articular surface at the cranial end of its body and two small articular hemispheres caudally, for the two concave articular cups at the cranial end of the urostyle. The articular area of each hemisphere is bigger than that of each articular cup on the urostyle, so that only a portion of it comes into contact with the cup in any given position of the joint. The two hemispheres are separated by a narrow rough non-articular interval. The sacrum articulates with the urostyle by two separate synovial joints; it also articulates with the hip bones by its stout, dorsally directed transverse processes.

The urostyle, or os coccygeum, is an unsegmented rod-like/

rod-like bone, which constitutes nearly half the length of the vertebral column. It is thick and broad at its cranial end but caudally it gradually becomes narrower until eventually it is succeeded by a small unsegmented rod of cartilage. The expanded cranial end of the urostyle has two cup-shaped articular surfaces for the hemispheres at the caudal end of the ninth vertebral body. A small rough non-articular area separates the two articular cups.

The sacral vertebra, the urostyle and the elongated hip bones together constitute the pelvic girdle.

The only noticeable curvature of the vertebral column is its dorsal convexity, the most prominent part of which is at the articulation of the sacrum with the urostyle.

The articular surfaces at the cranial and caudal ends of each vertebral body are covered with a layer of hyaline cartilage (Fig.7). The cartilages covering both concave and convex surfaces are thickest at the centre and thinner towards the periphery. The free surface of the cartilage (i.e., the surface looking towards the joint cavity) is a thin layer in which the cells are flattened and small and are disposed with their long/

long axes parallel to the articular surface; a few collagen fibres are evident in this layer. The next layer consists of rounded cells arranged in groups, and forms the main part of the cartilage (Fig.7). The deepest part of the cartilage, on the other hand, gradually merges with the zone of growth at the cartilaginous end of the vertebral body. Peripherally the articular cartilage gives attachment to the synovial membrane and gradually merges with it.

At the centre of the articular cartilage, or a little dorsal to this position, there is a small irregular depressed area; this area at the ends of contiguous vertebral bodies is the site of degeneration of the central ligament, which connects the adjacent vertebrae in early life. Such an area or degenerated ligament is not found in the joints between the ninth vertebra and the urostyle. The central ligament, connecting the eighth vertebra cranially with the caudal end of the seventh, and caudally with the cranial end of the ninth has been found to be present within the three year old specimens examined (Fig.8), although I have not found any reference to this in the literature. Each central ligament is formed by the continuity of the central portions/

portions of the contiguous articular cartilages, around a central mass of homogeneous substance containing some collagen fibres (Figs. 8 and 9). The collagen fibres run along the long axis of the column, a little dorsal to its central axis (Fig.8). The homogeneous tissue and the collagen fibres of the central ligament extend into the middle of the adjacent vertebral bodies to become continuous with the intravertebral remnant of the notochord. Surrounding the central ligament, there is a periligamentous annular space, that is the synovial cavity (Figs. 8 and 9). Thus it is clear, that the central ligaments connecting the eighth vertebra with its adjoining vertebrae persist even in the adult frog, when the same ligament in the other vertebral joints has undergone degeneration, making the articular surfaces of the vertebral bodies absolutely free.

Even though the intervertebral portion of the notochord and the central ligament have degenerated and disappeared almost completely, the central parts of the vertebral bodies still enclose, even in adult frogs, an isolated vestige of notochord (Fig.7). This remnant of notochord is formed of a homogeneous mass of mucoid substance and a small network of thin fibres enclosing big/

big spaces. On the fibres of the network there are a few large nuclei, though the cell outline is not exhibited. This notochordal remnant lies dorsal to the central axis of the vertebral body.

The articular capsule of each joint between the vertebral bodies consists of an outer fibrous layer, the capsular ligament, and an inner layer of synovial membrane.

The capsular ligament surrounds each joint, and is attached to the margins of the articular surfaces of the adjacent vertebral bodies, and is continuous with the periosteum there (Fig.7). It is strengthened ventrally by the ventral longitudinal ligament, while dorsally it is thin. On the sides the capsular ligaments are reinforced by strong lateral intervertebral ligaments. The capsular ligaments of the two joints between the ninth vertebra and the urostyle are loose and lax.

The synovial membrane lines the inner surface of the capsular ligament of each joint. It extends from the margin of the articular cartilage of one vertebra to the margin of the articular cartilage of the adjoining one (Fig.7). Histologically, the synovial layer is fibrous in type. The cells which occur on the surface of the synovial membrane are flattened or spindle-shaped fibroblasts/

fibroblasts, but do not usually form a continuous layer. In some areas the cells are widely separated with connective tissue fibres interposed between them, in other areas the cells are spread in a single thin layer, or may even be crowded together, two or three deep. No demonstrable elastic fibres are seen either in the capsular ligament or in the synovial membrane. A few blood vessels are seen to be present between the deeper fibres of the synovial membrane and the capsular ligament, especially on the ventral aspect. Within each of the joints between the ninth vertebra and the urostyle, a long fold of synovial membrane projects from the dorsal aspect and lies between the hemisphere and the cup.

The ventral aspects of the bodies of the vertebrae and the intervertebral joints are connected together by a white, sheet-like fibrous membrane, called the ventral longitudinal ligament. This ligament begins at the base of the skull and extends to the cranial end of the urostyle, where it blends with the periosteum. The ligament becomes gradually broader and thicker as it is traced from the cranial to the caudal end. It is firmly attached to the capsular ligament, but only loosely attached to the middle of the vertebral bodies. The fibres/

fibres run longitudinally in a cranio-caudal direction. At the sides, opposite the intervertebral joints, the fibres of the ligament are continuous with the fibres of the lateral intervertebral ligaments.

No distinct longitudinal ligament has been defined on the dorsal aspect of the vertebral bodies and intervertebral joints.

On the lateral side of each joint, between the bodies of the vertebrae, there is a small white fibrous ligament, and this may be called the lateral intervertebral ligament. No reference has been found to these ligaments but they are definite and well-defined structures. Each ligament is attached to the lateral margin of two adjacent vertebral bodies, just outside the attachment of the capsular ligament. Ventrally its fibres are continuous with the fibres of the ventral longitudinal ligament, and dorsally the fibres blend with the capsular ligament. Laterally, the attachments of each intervertebral ligament extend on the vertebral bodies to the roots of the transverse processes, so that the ligament forms the ventral boundary of the intervertebral foramen, giving exit to a spinal nerve.

A short but strong fibrous ligament is attached to the/

the roughened intervals between the hemispheres of the ninth vertebra and the cups of the urostyle. The fibres of this ligament blend with the capsular ligament on either side, and ventrally its fibres are continuous with those of the ventral longitudinal ligament.

THE INTERVERTEBRAL JOINTS OF REPTILIA

Observations:

CLASS - Reptilia

SUB-CLASS - Diapsida

ORDER - Squamata

SUB-ORDER - Lacertilia

SPECIES - Lacerta viridis (Green Lizard)

AGE - Adult

WEIGHT - 17 gms.

LENGTH OF VERTEBRAL COLUMN - 28.2 cm.

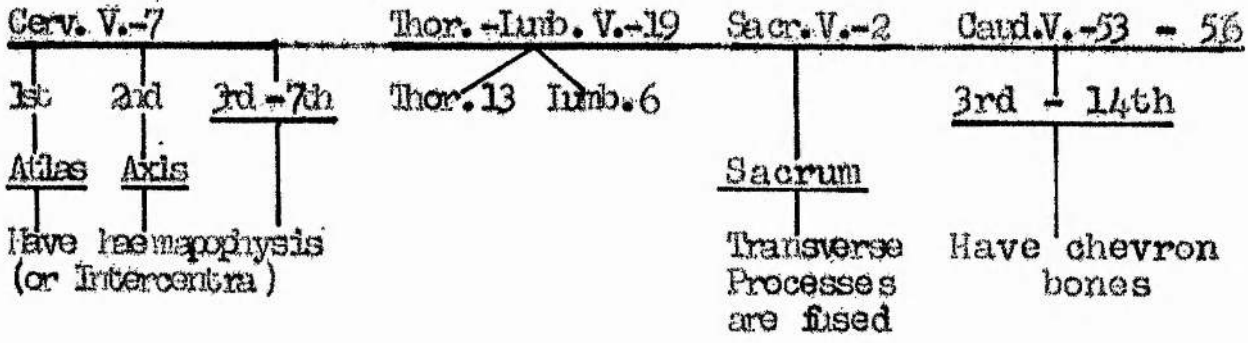
LENGTH OF CERVICAL REGION - 1.5 cm.

LENGTH OF THORACO-LUMBAR REGION - 5.0 cm.

LENGTH OF SACRAL REGION - 0.4 cm.

LENGTH OF CAUDAL REGION - 21.3 cm.

The vertebral column of the adult Lacerta viridis is very long and is composed of some eighty-one to eighty-three vertebrae, all free. The column is grouped into five regions as follows:



The/

The joints between the vertebrae are arranged on a common plan, except those existing between the first two cervical vertebrae, which form a special articulation.

The joints between the bodies of adjacent vertebrae are secondary cartilaginous joints, or amphiarthroses, where the bodies are connected together by intervertebral fibro-cartilaginous disks and by ligaments. The vertebral arches, on the other hand, are united by plane synovial joints.

The basic character of the vertebral bodies (except the first two cervicals) is common throughout the length of the vertebral column.

Each vertebral body is a short cylinder of bone with expanded cranial and caudal ends, the former being more prominent than the latter. The bodies of the vertebrae in the cervical and the sacral regions are shorter than the others. The caudal vertebrae, however, have much longer bodies, but these become gradually smaller as the caudal end of the tail is reached. About half the distal caudal vertebrae are formed only of rod-like bodies.

The cranial and the caudal end of each vertebral body is articular; of the two the cranial end is deeply concave to form a socket, while the caudal end is highly convex to resemble/

resemble a ball. The concave socket of one vertebra receives the rounded ball of the other just adjacent to it, and between the two a fibro-cartilaginous disk is interposed (Figs. 10 and 13).

The concave articular surface at the cranial end of each vertebral body is transversely oval and looks both cranially and ventrally. Its thinner dorsal margin projects further in a cranial direction than the ventral margin (Figs. 10 and 11). The articular surface at the caudal end of each vertebral body is convex both from side to side and dorso-ventrally; it is wider transversely, and this surface extends more on the dorsal aspect of the bone than on the ventral. The curvatures on the articular surfaces of the bodies of the distal caudal vertebrae are much less pronounced than those in other regions.

In the cervical region, on the ventral aspect of each intervertebral joint, there is a small almost pyramidal nodule of bone in the median plane, which is called the haemapophysis or intercentrum (Fig. 13). The base of each haemapophysis is connected with the ventral aspects of the articular ends of two contiguous vertebrae by fibro-cartilage and by short fibrous ligaments. Further, the haemapophyses are connected with each other by thin fibrous bands/

bands (or threads).

In the caudal region, however, ventral to each intervertebral joint between the third to the fourteenth caudal vertebrae, there is a Y-shaped piece of bone, called the 'chevron bone'. The limbs of the 'Y' are connected to the ventrilateral aspects of each joint by part of the fibro-cartilaginous disk and by ligaments, similar to the haemapophysis of the cervical region. The stem of the 'Y' is directed ventrally and caudally and is called the haemal spine. The space enclosed by the vertebral column and the chevron bones forms a protective canal for the caudal blood vessels.

In the middle of the body of each caudal vertebra, there is an unossified transverse septum which easily breaks off.

Intervertebral Disk:

The convex and concave surfaces of the adjacent vertebral bodies are united together by a fibro-cartilaginous intervertebral disk. Ventrally the disk extends on the convex articular surface beyond the limit of the concave surface of the adjoining vertebral body (Figs. 10 and 13). It is thickest at its centre and thinner towards the periphery, although the thickness of the disk varies in different/

different regions of the vertebral column. In fact, the disk is thickest in the caudal region and thinnest in the sacral region.

The ventral part of the intervertebral disk, in the cervical region, connects the haemapophysis with the ventral part of each convex articular surface (Fig. 13). Similarly, in the caudal region, the two limbs of the chevron bone are connected to the sides of the convex articular surface by the ventrilateral parts of the disk.

Structurally, the disk is composed of fibro-cartilage which is more fibrous than cartilaginous (Figs. 10, 13 and 14). The fibres are short and pass through the substance of the disk from side to side, lying parallel to the cartilaginous ends of the bodies of the vertebrae, which meet at the joint. The fibres predominate at the periphery of the disk, where they remain remarkably distinct from the fibres of the intervertebral ligament (Figs. 11 and 12). Most of the fibres of the disk terminate by passing into the matrix of the cartilaginous ends of the vertebral bodies, but a few fibres lying between these follow the curvature of the disk (Figs. 13, 14 and 15). In the cervical and caudal regions, in addition, the fibres of the disk are similarly inserted into the cartilaginous ends of the/

the haemapophysis and chevron bone respectively.

In the adult specimens examined, the central part of the intervertebral disk, in all the regions of the column, presents a very small homogeneous mass irregularly enclosed by a spiral thread of tissue (Figs. 14 and 15). This homogeneous tissue contains a few collagen fibres, which pass for a short distance along the notochordal tract, into the cartilaginous ends of the adjacent vertebral bodies (Figs. 15 and 16). This tissue represents a vestigial remnant of notochord in the intervertebral region. Vertebrally, however, no notochordal remnant is observed.

Intervertebral Ligament:

The margins of contiguous vertebral bodies are intimately connected together by a strong and thick fibrous ligament, which is termed the intervertebral ligament (Figs. 10 and 11). This ligament is comparable with a capsular ligament. Superficially, the intervertebral ligament blends intimately with the longitudinal ligaments but its deep surface is quite distinct from the peripheral margin of the intervertebral disk (Fig. 12). The dense nature of the collagen fibres of the ligament is characteristic.

Ventral and Dorsal Longitudinal Ligaments:/

Ventral and Dorsal Longitudinal Ligaments:

Two longitudinal ligaments are present, one on the ventral aspect and the other on the dorsal aspect of the vertebral bodies and intervertebral joints. Each ligament connects the bodies of the vertebrae and the intervertebral ligaments together.

The ventral longitudinal ligament (Fig. 10) is a strong white glistening fibrous cord, that extends from the tip of the haemapophysis between the sixth and the seventh cervical vertebrae to the ventral surface of the last caudal vertebra. The ligament is very narrow and is loosely attached to the middle of the ventral surface of the vertebral body but, in the intervertebral region, it is broader and thicker and is intimately attached to the intervertebral ligaments and to the margins of the adjoining vertebral bodies. The ligament has a characteristic, beaded appearance.

The dorsal longitudinal ligament is a thin, more or less translucent, fibrous structure that lies on the floor of the neural canal (Fig. 10). It extends from the dorsal surface of the body of the axis to the dorsal surface of the last caudal vertebra. It is very loosely attached to the middle of the dorsal surface of the vertebral bodies/

bodies but is wider and firmly attached to the inter-vertebral ligaments and to the margins of the adjoining vertebral bodies.

Each ligament consists of longitudinal fibres but, in the intervertebral region, the deepest fibres blend with the intervertebral ligament (Figs. 11 and 12).

THE INTERVERTEBRAL JOINTS OF AVES

Observations:

CLASS - Aves

SERIES - Carinatae

ORDER - Galliformes

SPECIES - Gallus domesticus: Common Fowl (Brown Leghorn/light sussex)

AGE - 2 years

WEIGHT - 4 lbs.

LENGTH of the Vertebral Column = 43.0 cm.

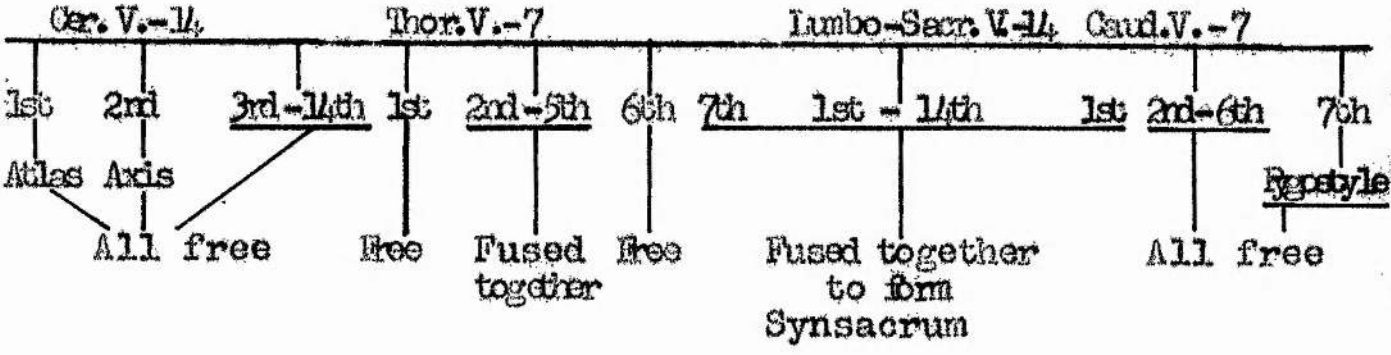
" " " Cervical region = 21.3 cm.

" " " Thoracic " = 8.1 cm.

" " " Lumbo-sacral " = 7.6 cm.

" " " Caudal " = 6.0 cm.

The vertebral column of the adult fowl is formed of forty-two vertebrae, which are distributed in the different regions (Fig. 17) as follows:



In/

In adult birds there is a great difference in the type of joint occuring between the bodies of the vertebrae and for that reason the joints of the different regions have to be considered separately. The different types of joints present in the column are:

1. Synovial joints,
2. Secondary cartilaginous joints, and
3. Synostosis.

In addition to the above joints, the arches of the vertebrae articulate with one another by a series of synovial joints.

The joints between the atlas and the axis form special articulations, and are not included in this investigation.

Cervical Region:

In the adult fowl the cervical region constitutes a long freely movable part of the vertebral column. The length of the cervical region in those adult birds examined, is almost half the total length of the column (43.0 cm.). This region has a well-marked ventral convexity at about its middle, with ventral concavities both cranial and caudal to this mid-region flexure.

The cervical region consists of fourteen vertebrae, all/

all free (Fig. 17), and two distinct groups of joints exist between them. There are (1) ventral joints between the bodies of the vertebrae, and (2) dorsal joints between the processes of the arches of the vertebrae.

The joints between the bodies of the cervical vertebrae form 2nd to 14th, both inclusive, may be classified as saddle-type synovial joints (articulatio sellaris).

Each joint cavity is incompletely divided into a cranial and a caudal portion by an intervertebral fibro-cartilage or meniscus, which lies between two adjacent vertebral bodies.

Each cervical vertebra is short and is constricted at its middle; its cranial and caudal articular ends are expanded. Each articular surface of the vertebral body is saddle-shaped or heterocoelous, the cranial articular surface being convex dorso-ventrally and concave from side to side, while the caudal surface is the reciprocal of this.

The cranial and caudal articular surfaces are each covered with a layer of hyaline cartilage, which is thickest at its centre and thinner towards the periphery, as/

as seen in sagittal sections (Figs. 18 and 19). The free surface of the cartilage is somewhat uneven and irregular and shows a layer of fibro-cartilage (Figs. 20a and 20b), which, at the periphery, is continuous with the synovial membrane. In an old bird of 2 years, the free surface of the articular cartilage shows roughening and fraying, especially located in the ventral part of the convex surface as shown in sagittal sections (Figs. 18, 20a and 20b). The rest of the articular cartilage presents a characteristic histological picture (Figs. 19, 20a and 20b). The cartilage of adult bird is less cellular than that of a young chicken, and the cells are arranged in groups; the number of cells enclosed within a single capsule is, however, greater than that in the cartilage of young birds. Cartilage cells of different sizes are found disposed throughout the cartilage, but the biggest ones are present in its deepest part. The matrix of the cartilage is notably heterogeneous in character (Figs. 18 and 20a). The intercellular substance immediately surrounding the capsules of the cartilage cells is especially basophilic, but the other parts of the matrix show a decline in basophilia. Signs of calcification are noted in different/

different parts of the cartilage, especially in its deeper zone, and it shows fibrillation at certain places with visible and unmasked collagen fibres in the matrix (Figs. 20a and 20b). Also the cartilage exhibits occasional fissures and clefts, mostly found in its deepest part, and these communicate with the marrow cavity of the underlying bone. The zones of proliferation and growth are not seen at the ends of the vertebral body.

Articular Capsule:

The articular capsule reveals an outer fibrous layer, the capsular ligament, and an inner layer of synovial membrane.

The capsular ligament is a distinct fibrous sheath and is attached to the margins of the articular surfaces of the adjoining vertebral bodies (Fig. 18). It is thicker ventrally and on the sides, but is thinner and somewhat translucent dorsally. Ventrally, in the middle line, the capsule is strengthened by a narrow fibrous band that extends between the two adjacent hypapophyses. The rest of the capsule, ventrally and on the sides, is supported by well-developed neck muscles.

The/

The synovial membrane lines the inner surface of the capsular ligament, except where the latter provides an attachment for the intervertebral meniscus (Figs. 18 and 19). It ceases at the margins of the articular cartilage at the ends of the adjoining vertebral bodies (Fig. 18). At the site of attachment of the meniscus to the capsular ligament, the synovial membrane becomes continuous with the fibro-cartilaginous tissue of the meniscus. At the junction of the synovial membrane with the articular cartilage, the synovial cells merge with the chondrocytes. At this site occasionally a small fold of synovial tissue overlies the articular cartilage for a short distance. This fold is also present at places as a sessile or pedunculated mass; the areolar tissue at the base of these pedunculated masses changes abruptly into fibrous tissue, and this latter eventually merges with the peripheral margin of the articular cartilage. One or two small synovial folds project inside the joint cavity from the inner surface of the capsular ligament (Fig. 21). The synovial membrane consists of cells, which are mainly fibrous, and are arranged in two, three or four layers. These cells are lying either on the fibrous capsule or on a layer of areolar/

areolar and adipose tissue.

Small blood vessels are present at the peripheral margin of the articular cartilage where the synovial membrane merges with it, and also between the two layers of the articular capsule.

Intervertebral Meniscus:

Within each intervertebral joint in the cervical region, there is an incomplete fibro-cartilaginous meniscus. Each meniscus is a ring-like structure with an oval aperture at its middle, which is nearer the ventral than the dorsal aspect. The peripheral margin of the meniscus is thick and is attached to the capsular ligament (Figs. 18 and 19); the inner margin, on the other hand, is thin, concave and free, and it forms the boundary of the central aperture. The cranial and caudal surfaces of the meniscus conform in shape to the articular surfaces of the vertebral bodies which form the joint. Structurally, the peripheral part of the meniscus is mainly fibrous but the inner part is fibro-cartilaginous (Figs. 18 and 19).

Thoracic Region:

The thoracic region of the vertebral column forms

a/

a somewhat stable and rigid segment comprising about one fifth part (8.1 cm.) of the entire column. It forms the roof of the thoracic cavity, and does not present any noticeable curvature.

This region consists of seven thoracic vertebrae; of these, the second to the fifth vertebrae are fused together by synostosis, and the fusion lines are distinguished, ventrally and on the sides, by transverse ridges. The first and sixth vertebrae, on the other hand, are free (Fig. 17), and form saddle-type synovial joints with their adjacent vertebrae. The seventh thoracic vertebra, however, is ankylosed with the lumbo-sacral mass of vertebrae.

The articular surfaces are saddle-shaped, as in the cervical vertebrae, but the curvatures are not so prominent. Furthermore, the articular surfaces are broader from side to side than dorso-ventrally, unlike the cervical vertebrae. Structurally, the articular cartilages exhibit the same histological picture as they do in the cervical region (Figs. 20a and 21).

The capsular ligaments which connect the body of the sixth thoracic vertebra with that of the fifth, cranially, and the seventh, caudally, are strong, white, glistening tough fibrous sheaths. These are thicker ventrally/

ventrally and on the sides, and are not covered by any muscle. The hypapophyses of the thoracic vertebrae are connected together in the median plane by a thin plate of bone.

No intervertebral meniscus is seen within the synovial joints of the thoracic region (Fig. 21).

The other features of the joints in this region are the same as those of the cervical.

Lumbo-sacral Region:

The lumbo-sacral region of the vertebral column is a single mass of bone, and forms about one-sixth (7.6 cm.) of the length of the whole column. It lies at the roof of the pelvic cavity.

This region consists of fourteen vertebrae, of which two are sacrals, but all are fused together to form the lumbo-sacral mass. This is fused with the seventh thoracic vertebra, cranially, and with the first caudal vertebra, caudally, to form the synsacrum (Fig. 17). The lines of fusion of the vertebrae are not distinguished but the segments are indicated by the intervertebral foramina. The iliac bones of the two sides are fused with the synsacrum.

Caudal Region/

Caudal Region:

The caudal region of the vertebral column is a short, curved and freely movable part, which forms the skeleton of the tail. It forms about one seventh (6.0 cm.) of the length of the whole column. It presents an uniform concavity which looks cranially and dorsally.

This region consists of seven caudal vertebrae; of these the first vertebra is fused with the lumbo-sacral mass, while the others are all free (Fig. 17). The last or the seventh caudal vertebra is shaped like a three-sided pyramid resembling a ploughshare and is, therefore, called the Pygostyle (Fig. 17); it is the largest of the caudal vertebrae and is probably formed by the fusion of several original distinct segments.

The joints between the bodies of the caudal vertebrae may be classified as secondary cartilaginous joints or amphiarthroses. A thick fibro-cartilaginous substance, the intervertebral disk, is interposed between two adjacent vertebral bodies.

Each caudal vertebra is a small and short cylinder of bone except the last or the seventh one, the character of which has already been described. The cranial and caudal surfaces of each vertebral body are slightly amphicoelous/

amphicoelous. Each of these surfaces is almost kidney-shaped in outline with its long diameter the transverse one and the hilum looking dorsally. Each surface is covered by a thin plate of cartilage, which separates the fibres of the disk from immediate contact with the bone.

Intervertebral Disks:

The intervertebral disks are bi-convex masses of fibro-cartilage that firmly connect the bodies of the adjacent caudal vertebrae together. The outline of each disk corresponds to that of the bodies between which it is interposed. The disk is deeper ventrally, and this accounts for the ventral convexity in this region of the column.

Each disk is formed of two tissue components, a narrow peripheral part of collagenous fibres and a thicker central part of fibro-cartilage (Fig. 22). This latter forms the chief bulk of the disk, and is further subdivided into an outer and an inner zone.

The peripheral part of the disk exhibits two zones; a small superficial zone of collagenous fibres, which mingle with the fibres of the longitudinal ligaments placed/

placed on the ventral and dorsal aspects of this region of the vertebral column, and a deeper zone consisting of concentric lamellae, which bind the adjacent vertebral bodies firmly and are attached to the cartilage plates therein (Fig. 22). The fibres, of which the lamellae are composed, are arranged in parallel bundles and pass obliquely between the opposing surfaces of two adjacent vertebrae. The fibre bundles of successive lamellae cross in opposite directions being disposed like a letter 'X'. These fibres, ventrally and dorsally, are thin and closely packed together, while on the sides, they are much thicker and more widely spaced.

The central fibro-cartilaginous component forms the principal part of the disk and in it the fibre architecture is of an intricate character (Fig. 22). The outer zone of this part consists of dense bundles of collagenous tissue embedded in a matrix of cartilage, which is not prominent except in its inner layers. The fibres of the outermost laminae consist mainly of collagenous tissue but the majority, especially those near the inner zone, are formed of fibro-cartilage. There is no line of demarcation between the different components and zones of the disk, each merges gradually with the other/

other (Fig. 22); this feature becomes progressively less distinct in the column of older birds. The inner zone of the fibro-cartilaginous component occupies the middle of the disk and appears much less dense than the outer zone. It consists of irregularly arranged fine fibre bundles and numerous cartilage cells (Fig. 22). There is no comparable fibre architecture, the bundles of fibres coursing indiscriminately. The fibres at its outermost part gradually become dense and eventually merge with the outer zone. A few fibres pass towards the cartilage plates, into which they sink and have firm attachment. Occasional fissures and clefts of varying shape and size are present within the disk without any definite disposition (Fig. 22).

Longitudinal Ligaments:

In the caudal region, two longitudinal ligaments exist, one ventral and one dorsal, which extend over the ventral and the dorsal surfaces of the bodies of the vertebrae and the intervertebral disks, respectively. The ventral ligament is much thicker than the dorsal one. Each ligament extends from the caudal margin of the first caudal/

caudal vertebra to the cranial margin of the last. The ligaments are firmly attached to the intervertebral disks and to the margins of the adjoining vertebral bodies. The superficial fibres pass over several vertebrae but the deeper fibres blend with the fibres of the disk and with the periosteum of the adjacent vertebral bodies.

Moreover, a group of tail muscles forms an additional support for these joints.

Cartilage Plate:

The cartilage plates at the ends of the vertebral bodies present an almost identical histological picture as has already been observed in the articular cartilages of the synovial joints. Only, the ends of the fibres of the disk are inserted into the intervertebral face of the cartilage plate; moreover, the fibrillation is more marked here than in the cervical region.

AVIAN NOTOCHORD

ITS DEVELOPMENT AND FATE

In chick embryos and in post-hatched young chicken the notochord is a prominent structure throughout the entire length of the growing vertebral column, including both vertebral and intervertebral regions.

Moniliform Differentiation:

In a 3-day chick embryo, the notochord is a rod-like structure of uniform diameter throughout its entire extent, with tapering cranial and caudal ends. The post-cranial part of the notochord, which is the subject for the present investigation, lies between the spinal cord dorsally, and the sclerotomic mesoderm, ventrally, and this latter separates it from the dorsal aorta (Figs. 23a and 23b). The notochord, in an embryo of 10 days incubation, presents a moniliform appearance within the developing vertebral column. This feature of the notochord is characterised by an intravertebral constriction and an intervertebral dilatation throughout the column. This moniliform differentiation of the notochord in a 15-day embryo shows great alterations as compared with that of a 10-day embryo. In the cervical region, the notochord exhibits three dilatations and two constrictions within the body of each vertebra (Figs. 24a and/

and 24b). The intermediate of the three dilatations within the vertebral body is relatively large and fusiform in shape and, in an 18-day embryo, is surrounded by bone. Within the cartilage of the cranial and caudal ends of the vertebral body, the notochord shows smaller dilatations, there being one dilatation in each mass of cartilage (Figs. 24a and 24b). The constrictions correspondingly occur at the junction of the ossified area and the cartilaginous ends. In the thoracic, lumbo-sacral and caudal regions, on the other hand, the notochord is widely dilated intravertebrally and does not show these secondary dilatations (Figs. 25a and 25b). Intervertebrally, the notochord is constricted in all regions of the vertebral column but this is especially marked in the cervical region, where the constriction extends both cranially and caudally into the articular cartilages of the adjacent vertebral bodies (Figs. 24a and 24b). This intervertebral part of the notochord, surrounded by cartilaginous tissue, constitutes the central ligament, which connects the adjacent vertebral bodies of the cervical and the free vertebrae of the thoracic region together (Figs. 26a, 26b and 30). In the other regions of the column, the intervertebral/

intervertebral notochordal constrictions are seen to persist until the 25th day, running through the middle of the cartilaginous disks joining the vertebral bodies (Figs. 29, 33a and 33b). The moniliform appearance of the notochord is found to exist in the young chick for about a month after hatching, although the intervertebral portion gradually disappears. The central ligament, on the other hand, degenerates and disappears first in the cervical region on the 10th day after hatching (Figs. 28a and 28b), while in the thoracic region, it does not disappear until the 20th day (Fig. 31).

Segmental Curvatures:

The notochord in a chick embryo of 3 days incubation is a straight rod and does not present any curvature (Fig. 23a). But, in a 10-day embryo, the notochord is characterised by the presence of segmental curvatures; these curvatures are convex ventrally in the intervertebral regions, and concave ventrally within the substance of the vertebrae. In a 15-day chick embryo, although the notochordal curvatures remain the same in the cervical region (Fig. 24a), in the thoracic, lumbo-sacral and caudal regions of the column the notochord is concave ventrally/

ventrally in the intervertebral portion and convex ventrally within the vertebral bodies. The curvatures are not so well-marked in the lumbo-sacral and caudal regions as they are in other regions of the column.

Regional Curvatures:

In addition to segmental curvatures the notochord also possesses regional curvatures in relation to the central axis of the vertebral column. This regional curvature is a characteristic feature in birds and the other vertebrates, which I have examined.

In the cranial part of the cervical region, the notochord lies a little ventral to the central axis of the column but, in the caudal part, it is located almost in the central axis of the vertebral bodies (Figs. 24a and 26a). In the thoracic region, the notochord deviates dorsally from the central axis (Fig. 30) and it retains this position, until the caudal part of the lumbo-sacral region is reached. Finally it is located almost in the central axis of the caudal region until the end of the pygostyle.

Structure:

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In a 3-day chick embryo the notochord consists of a peripheral zone - the notochordal sheath - and a middle cellular zone. The notochordal sheath is a very thin, homogeneous structure of uniform thickness and is present throughout its entire extent. Only in the tail region, it becomes gradually thinner and is hardly recognisable from the rest of the notochord. Later, in an embryo of 15 days incubation, the sheath presents a variable thickness, being thicker intervertebrally and thinner intravertebrally. The homogeneous character of the sheath gradually merges with the matrix of the surrounding cartilage of the vertebral body. The intravertebral portion of the sheath is discontinuous in places and this is especially marked in a newly hatched chick, where bone formation is observed on its wall in the middle of the vertebral body (Fig. 24a). At this stage no distinct sheath is recognisable; the peripheral zone of the notochord consists of a homogeneous tissue, which closely resembles mucoid material in character, and this is constantly observed with advancing age, when a diminution and degeneration of the cells in the middle zone is also noticed. Even in a young chick of 25 days, the remnant of the notochord perists as a small mass of mucoid material seen/

seen at the cartilaginous ends of the vertebral bodies of the cervical and free vertebrae of the thoracic regions (Figs. 31, 32a and 32b); in the caudal region, however, it perists in the intervertebral disks (Figs. 29, 33a and 33b) but is later invaded by the surrounding fibro-cartilage (Fig. 34).

The middle cellular zone of the notochord in a 3-day chick embryo consists of notochordal cells, which show varying degrees of vacuolisation in different regions of the column (Figs. 23a and 23b). In the cervical and cranial part of the trunk region, the cells exhibit vacuoles which vary in form and size but most of the central cells are polygonal. The peripheral cells, on the other hand, are smaller and do not show any noticeable vacuolisation; these cells are arranged in one or two rows with their long axes disposed across the notochord and closely resemble columnar epithelium. In the hinder part of the trunk and in the caudal region, the notochordal cells are circular or oval in outline and do not show any vacuolisation. The nuclei are more numerous in the peripheral layer than in the centre. In the transitional area between the cranial and caudal parts of the trunk region, only isolated central cells show vacuolisation and/

and the vacuoles are smaller in size than those in the cervicoal region. During the process of normal development, the notochordal tissue regresses; this is noticed by the 10th day of incubation. This change is brought about by nuclear degeneration but also by a decrease and degeneration of the vacuolated cells; these changes are more marked intravertebrally than intervertebrally, where a few isolated notochordal cells persist . In the 15 day embryo, the notochord is again cellular, and the cells resemble, more or less, those of hyaline cartilage. In the inter-vertebral regions, the notochordal cells are closely aggregated and are disposed cranio-caudally within the central ligaments (Figs. 24a and 24b) and cartilaginous disks (Figs. 25a and 25b). Intravertebrally, however, the cells are vacuolated and only a few protoplasmic cells are present towards the periphery. Ossification has supervened on the wall of the central dilated part of the notochord within the vertebral body and this is well-marked in a newly hatched chick. At this stage the intravertebral portion of the notochord consists of a loose network of protoplasmic threads with sparse nuclei disposed in the knots. In both the vertebral and inter-vertebral portions of the notochord fine indistinct fibres are/

are evident in the homogeneous matrix in which notochordal cells lie. In the caudal region of the newly-hatched chick, the notochord within the intervertebral disk consists of a mass of homogeneous tissue with a few cells and fine fibres scattered in it, and between these are a few small, irregular spaces. By the 10th day after hatching, the intervertebral portion of the notochord within the central ligament shows signs of degeneration and disappearance (Figs. 28a and 28b) but a remnant of the notochord persists at the cartilaginous ends of the vertebral bodies only, as small streaks of mucoid material, along with notochordal tract (Figs. 32a and 32b). Neither the central ligaments nor the mucoid streaks of remaining notochordal tissue persist in the vertebral column of the adult bird.

OBSERVATIONS ON THE INTERVERTEBRAL JOINTS OF YOUNG CHICKEN FROM THE FIRST TO THE THIRTIETH DAY AFTER HATCHING

The joints of the bodies of the vertebrae are clearly distinguished in the vertebral column of the young chicken, at all ages from one day to thirty days after hatching. Even in a newly hatched chick, these joints, in the cervical region, are of the synovial saddle type; the first and the sixth thoracic vertebrae form similar joints with their adjoining vertebral bodies. The bodies of the 2nd to 5th thoracic vertebrae and those in the other regions of the column are connected together by a mass of cartilage between the two adjoining bodies (Figs. 27a and 27b); these cartilages in the caudal region are transformed later into fibro-cartilaginous disks (Fig. 34) while in the thoracic and lumbo-sacral regions they undergo synostosis.

In a newly-hatched chick the vertebral bodies are very short, and each body is easily recognised as a disinct component in all the regions of the column. Each vertebral body is mainly a cartilaginous structure, only the middle portion shows both perichondral and endochondral ossification. By the time the chick becomes 20 to 30 days old, each vertebral body is highly elongated, and is expanded at its cranial and caudal ends. The ossification extends almost to the ends of the vertebral body,/

body, leaving only small cartilaginous zones of proliferation and growth. Each cranial and caudal end of the cervical and free thoracic vertebrae is covered with a layer of hyaline cartilage. The articular surfaces of these vertebral bodies are heterocoelous or saddle-shaped, even in a newly-hatched chick, but they become well-marked with deeper curvatures from ten days onwards after hatching. The middle portions of the articular surfaces of the adjacent vertebral bodies in these regions are connected together by the central ligament. Each central ligament is formed by the continuity of the middle portion of the articular cartilage of two adjacent vertebral bodies with a core of notochordal tissue in its middle (Figs. 26a and 26b). This ligament is surrounded by the cavity of the inter-vertebral synovial joint. By the second week, the central ligament undergoes degeneration and eventually disappears, and this is first evident in the cervical region of the vertebral column (Figs. 28a and 28b).

In the young chicken a median cartilaginous hypapophysis is present on the ventral aspect of the cervical and all the thoracic vertebrae except the last one, and these are connected together by thin fibrous bands.

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The hypapophyses of the thoracic vertebrae are also interconnected by cartilaginous structures. By the 20th day, the ossification of the vertebral body extends to the root of the hypapophysis but the tip remains cartilaginous for some time more.

In the newly-hatched chick, the articular cartilages of the synovial joints are rich in young and immature cartilage cells, while the amount of matrix present is relatively small. Beginning at the free surface of the articular cartilage and proceeding in the direction of the bony end, the cells undergo a gradual transformation. Near the surface of the cartilage they are spindle-shaped or almost flattened and very similar to ordinary fibrocytes. As a rule, one or at most two layers of such cells are present. These, towards the periphery, become continuous with the synovial membrane of the joint capsule and, in the middle, with the central ligament (Figs. 26a and 26b). The deeper cells of the cartilage are rounded and arranged, for the most part, singly lying very close together. This zone represents the main body of the articular cartilage. In the very deepest part, the cells are continuous with those of the zone of proliferation at the cartilaginous end of the vertebral body. The notochord passes through the/

the cartilage and the central ligament a little ventral to the central axis of the cervical region (Figs. 26a and 26b). From the fourth day onwards, the cells of the articular cartilage enlarge and become arranged in pairs. With advancing age, the appearance of the articular cartilage is greatly changed and it is proportionately reduced in thickness. The cells on the free surface are now more distinct but as numerous still as at the earlier age; however, the cells of the deeper layer decrease in number, and the cartilaginous ground substance is correspondingly increased. After the degeneration and disappearance of the central ligament, a remnant of notochord is seen to persist, even in a 30-day chick, as a small streak of mucoid material within the articular cartilage and the cartilaginous end of the vertebral body (Figs. 32a and 32b).

The articular capsules of the synovial joints of the cervical and thoracic regions consist of an outer layer, the capsular ligament, and an inner layer of synovial membrane. The capsular ligament, in a newly hatched chick, is thin and consists of young fibroblasts and a few collagen fibres (Figs. 26a and 26b). From the fourth day onwards, the ligament becomes gradually thicker and thicker and is/

is formed more of collagen fibres than of cells, which become spindle-shaped with thin and flat nuclei. Except for the presence of more collagen fibres, the structure of the capsular ligament remains more or less the same throughout. No elastic tissue fibres are observed in the capsular ligament.

In the new-born chick, the synovial membrane of the joint is especially thin and delicate, and the scattered lining areolar type cells are often connected with each other by tenuous strands. In some specimens, a similar delicacy of structure is present at its junction with the intervertebral meniscus, but in others the tissue is densely cellular in this location. The synovial layer is continued on the surface of the meniscus for only a very short distance, but this is not a constant feature in all the specimens examined. Small folds of synovial membrane are present between the peripheral margin of the meniscus and the articular cartilage (Figs. 28a and 28b). These folds enclose small blood vessels and a few collagen fibres. No fundamental change in the synovial tissue is noted during the later period of growth, except for the change from areolar to fibrous type synovial cells lining the membrane, and this character may be ascertained even in/

in a 20 day chick. The transition from the almost collagen free, vascular synovial layer to the densely collagenous meniscus is particularly striking at this age. Later, collagen fibres become more abundant in the synovial membrane of the older specimens, but fail by far to reach the density of the capsular ligament and the meniscus. The fibres are grouped into small irregular strands which lie close to the joint cavity, especially in those areas lined by only a few surface cells. The vascularity of the synovial membrane is increased and becomes more marked with advancing age. No definite elastic fibres are distinguished in the synovial tissue, although they are present in the walls of the larger vessels.

The intervertebral meniscus in the cervical region incompletely divides each joint cavity between the vertebral bodies into a cranial and a caudal portion. Each meniscus presents an oval aperture, which is nearer the ventral than the dorsal part of the joint with its long diameter lying dorso-ventrally. In the chick embryos and post-hatched young chicken, until the 10th day, the oval aperture of the meniscus gives passage to the central ligament of the joint (Figs. 26a and 26b). At a very early stage, the meniscus is indicated by closely packed cells, the long axes/

axes of which are transverse to that of the column. A few strands of collagen fibres are present especially at its peripheral margin. The surface cells are thin and flat, in contrast to the rounded and more deeply placed fusiform cells. With advancing age, the cells in the meniscus increase in size and the collagen fibres become more prominent, especially at the junction with the capsular ligament. Although the cells covering the menisci often show an orientation which resembles that of the cells of the synovial membrane, in no instance is the tissue immediately subjacent to the surface cells vascularised, except at the attachment of the meniscus to the capsular ligament. In the subsequent stages of growth, there is not only abundance of collagen fibres in the meniscus but also the presence of cartilage cells, especially observed towards the inner part of the meniscus. No intervertebral meniscus has been observed in the synovial joints between the bodies of the thoracic vertebrae (Fig. 30).

Small blood vessels are present at all ages of the growing chick, and they increase in number and size with advancing age. Three situations are noticed where blood vessels are almost constantly seen, namely, (1) at the peripheral margin of the intervertebral meniscus, between it/

it and the capsular ligament, (2) at the peripheral margin of the articular cartilage, where the synovial membrane merges with it, and (3) just deep to the surface layer of cells of the synovial membrane and within its folds as well.

The caudal region of a new-born chick presents a cartilaginous mass, which connects the bodies of adjacent vertebrae (Figs. 27a and 27b). This cartilaginous mass is the intervertebral disk. Each disk consists of hyaline cartilage and this is continuous, cranially and caudally, with the zone of proliferation at the ends of the adjacent vertebral bodies. The peripheral zone of the disk exhibits a few collagen fibres and young fibroblasts. The middle of each disk is traversed by the remains of the notochord and the tissue surrounding this is cartilaginous in character. With advancing age the peripheral zone of the disk develops closely aggregated collagen fibres while the inner zone, surrounding the notochord, becomes fibro-cartilaginous (Fig. 34), although only a few fibres are exhibited in the earlier stage until the 30th day. Still later, especially in the adult specimens, the inner zone of the disk is typically differentiated into fibro-cartilage (Fig. 22), which eventually invades the notochordal area; this has already been described in the previous chapter.

THE INTERVERTEBRAL JOINTS OF MAMMALIA

Observations:

CLASS - Mammalia

DIVISION - Theria (or True Mammal)

SERIES - Eutheria

SUB-SERIES - Unguiculata

ORDER - Rodentia

SPECIES - Mus norvegicus albinus (Albino rat)

AGE - Adult (1 yr.)

WEIGHT - 315 gms.

LENGTH of the Vertebral column - 37 cm.

" " " Cervical region = 2.5 cm.

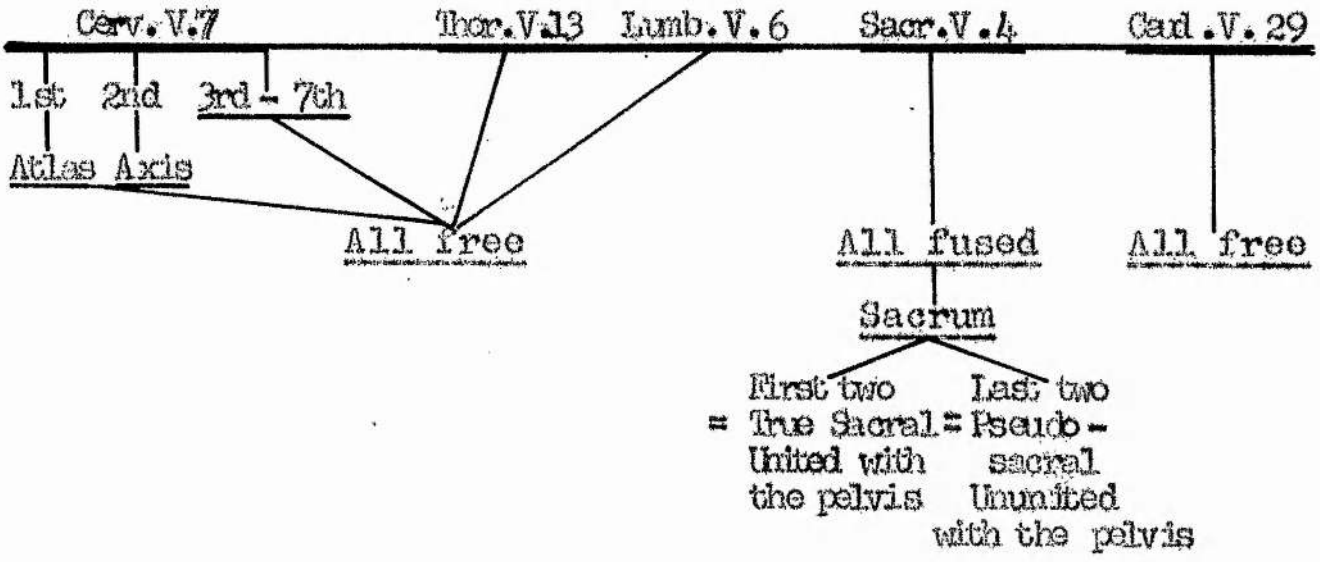
" " " Thoracic " = 5.9 cm.

" " " Lumbar " = 4.5 cm.

" " " Sacral " = 2.7 cm.

" " " Caudal " = 21.4 cm.

The vertebral column of the adult albino rat consists of a series of fifty-nine vertebrae, arranged in succession so that their bodies form a continuous rod. The column is distinctly divided into five regions:



The component vertebrae are so disposed that the column, when seen in profile, presents between the atlas and the tail, two curvatures, directed alternately downwards and upwards. Thus the last three or four cervical and the first three or four thoracic vertebrae form a curve, which is convex ventrally, while the thoracic, lumbar and the sacral vertebrae together form a curve, which is much less convex dorsally.

The joints between the bodies of the vertebrae form secondary cartilaginous joints, or amphiarthroses. The contiguous vertebral bodies, except the first two cervicals and all the sacrals, are connected together by a fibro-cartilaginous intervertebral disk and by ligaments.

The joints between the atlas and the axis form special articulations, and these are not included in this investigation./

investigation.

Each vertebral body is more or less cylindrical in form, although it is subjected to a wide range of variation, in shape and size, in different regions of the vertebral column of albino rat. The bodies from the third cervical to the first sacral increase gradually in size and weight, and all of them conform to a general basic plan. The cranial and the caudal surface of each vertebral body is more or less flat and roughened to provide attachment for an intervertebral disk. Ventrally, the body is convex from side to side and concave cranio-caudally, while dorsally, it is almost flat or very slightly concave.

The cervical vertebrae from the third to the seventh, both inclusive, have small, flat and wide bodies. The surfaces at the cranial and caudal ends of each vertebral body are oval in outline, with the transverse diameter greater than the dorso-ventral diameter. The presence of a small neuro-central lip, on the dorso-lateral margin of the cranial surface of each vertebral body, makes the surface transversely concave and slightly oblique in a dorso-ventri-caudal direction. The caudal surface of the vertebral body, on the other hand, is almost flat with a small, projectile ventral margin.

The/

The bodies of the thoracic vertebrae except the last two or three, which approach in character the succeeding lumbar vertebrae, are comparatively shorter. The cranial and the caudal surface of each body is vertically truncated, more or less flat and oval in outline. A very small depression is present in the middle of each surface.

The lumbar vertebral bodies are long, and are characterized by their large size. The cranial and caudal surface of each body is very slightly sloped caudally from the dorsal to the ventral margin. Each surface is oval in outline and presents a small depression at its centre.

Four sacral vertebrae are fused together to form a single composite bone, the sacrum. The fusion lines are indicated by transverse white ridges. The transverse processes of the first two sacral vertebrae articulate with the ilium.

The cylindrical bodies of the caudal vertebrae progressively increase in length but diminish in thickness, until the seventh or the eighth vertebra is reached when they gradually diminish in length also. The first four or five caudal vertebrae are comparatively shorter and broader/

broader than the rest. The terminal caudal vertebrae, on the other hand, consist of simple rod-like bodies only, and they are progressively reduced in size and complexity and vary greatly in number. The cranial and caudal surfaces of the first few vertebral bodies are circular in outline and their planes are disposed obliquely, each surface being sloped in a caudal direction dorso-ventrally. The surfaces of the other vertebral bodies are absolutely flat and vertical.

The cranial and the caudal surface of each vertebral body is covered with a thin epiphyseal plate (Fig. 35), and it is to this that the intervertebral disk is firmly attached.

In the caudal region of the vertebral column, small wedge-shaped chevron bones are present on the ventral aspects of the intervertebral joints, as far caudal as the 5th or 6th vertebra from the tip of the tail.

Intervertebral Disks:

The intervertebral disks are bi-convex, tough but elastic, and compressible masses of tissue of composite structure, and these form the chief bond of union between the vertebral bodies. Each disk presents a considerable thickness/

thickness and its outline corresponds to that of the surfaces of the vertebral bodies, between which it is placed.

Each disk consists of two principal parts, a peripheral white fibro-cartilaginous part, the annulus fibrosus, and a central soft, translucent, gelatinous part, the nucleus pulposus; the former firmly surrounds and braces the latter, and forms a little more than half the disk.

The disks are considerably thicker ventrally than dorsally except in the thoracic and caudal regions, where they are thicker dorsally than ventrally. In the caudal region, however, a small chevron bone is present, ventral to each intervertebral region, and this is firmly connected to the disk and adjacent vertebral bodies by strong fibrous ligaments.

The annulus fibrosus is a firm, dense structure of collagen fibres and cartilage cells. It exhibits two zones, an outer zone of densely aggregated fibres, and an inner zone of less dense fibro-cartilaginous tissue (Fig. 35). Both the zones of the annulus contain arched fibres, which at their terminations enter the matrix of the epiphyseal plates of the adjoining vertebral bodies (Figs. 35 and 36).

Ventrally/

Ventrally and dorsally the fibres are closely packed together, while laterally they become much thicker, more widely spaced and spread over a much larger area.

The fibres of the outer zone of the annulus run across the intervertebral space, following an outwardly convex course. The fibres of the various lamellae lie at angles with one another. Some fibres do not follow a simple arched course across the intervertebral space, but split away and subsequently join with the fibres of other bundles. A few fibres are seen to terminate in a forked manner, from the angle of which other fibres start. The fibrillar character of this dense bundle of connective tissue is almost lost in old rats where the fibres appear to be hyalinized (Figs. 37 and 39). Further, due to the coarsening of the fibres, no distinct fibre architecture is exhibited. The fibres terminate in the matrix of the epiphyseal plates, to which they are firmly anchored (Figs. 35 and 36). Ventrally and dorsally, the most superficial part of this zone is reinforced by the ventral and dorsal longitudinal ligaments.

The inner fibro-cartilaginous zone forms a considerable part of the annulus fibrosus (Figs. 37 and 39). It consists of a series of concentric lamellae, with cartilage cells in-

between/

between the fibres. The fibres of the different lamellae pursue an outwardly convex and oblique course from their attachments to the epiphyseal plates of the adjacent vertebral bodies. There is no clear line of demarcation between the two zones of the annulus fibrosus. The innermost part of the fibro-cartilaginous zone, which surrounds the nucleus pulposus, shows no lamination of its fibres, both the fibres and the cartilage cells being irregularly disposed (Figs. 37, 38 and 39). This area is clearly demarcated from the nucleus pulposus although ventrally and dorsally, as seen on median sagittal sections, a few fibres of the fibro-cartilaginous zone mingle with the peripheral part of the nucleus pulposus (Figs. 37 and 38). This encroachment of the fibro-cartilaginous zone of the annulus on the nucleus pulposus not only reduces the area of the latter but also makes its outline very irregular (Figs. 38 and 39).

The nucleus pulposus is a slightly bi-convex, white glistening body of a semi-gelatinous consistency. It is irregularly ovoid in shape and is placed nearer the dorsal than the ventral part of the disk. It is formed of a faintly basophilic homogeneous mucoid substance in which the chorda-reticulum is seen. The chorda-reticulum is/

is formed of an irregular network of thin fibres with big nuclei placed between them (Fig. 38). The proportion of chorda reticulum to mucoid material in the nucleus varies greatly. The nuclei are mostly oval in shape but the outline of the cells is not exhibited. The nucleus pulposus is enveloped by a thin fibro-cartilaginous layer, which eventually merges with the inner zone of the annulus fibrosus (Figs. 37 and 38). Fine interlacing fibres extend from the fibro-cartilage envelope into the nucleus pulposus (Fig. 38). This fibro-cartilaginous envelope separates the nucleus pulposus from the epiphyseal plates, cranial and caudal to it. Although a fairly sharp demarcation exists between the nucleus pulposus and the surrounding fibro-cartilage, the latter gradually encroaches on and its fibres are mingled with the peripheral part of the nucleus, as seen both ventrally and dorsally in median sagittal sections (Figs. 38 and 39).

Ventral and Dorsal Longitudinal Ligaments:

Two longitudinal ligaments exist, one ventral and one dorsal, which connect together the vertebral bodies and the intervertebral disks.

The ventral longitudinal ligament is a thin longi-

tudinal/

tudinal membrane extending over the ventral surfaces of the bodies of the vertebrae and intervertebral disks. It is continuous from the ventral arch of the atlas to the first segment of the sacrum. About the middle of the sacrum the ligament blends with the periosteum of that bone, but is again recognisable as a ligament on the ventral aspect of the caudal region. It is narrow at its cranial end, but gradually widens as it is traced caudally, until in the lumbar region it becomes again narrower and thicker. In the tail region, however, the ligament is interrupted by the chevron bones on the ventral aspects of the intervertebral joints. The fibres of the ligament are disposed longitudinally, and are attached firmly to the intervertebral disks and margins of the vertebral bodies, but somewhat loosely to the middle of the bodies. The superficial fibres are of variable length and run longitudinally, but the deep fibres are short and blend with the outer zone of the annulus fibrosus.

In the cervical region, the ligament is strengthened by the tendinous fibres of the longus colli muscles, in the lumbar region by the crura of the diaphragm and psoas muscles, and in the tail region by the strong tendinous fibres of the tail muscles.

The/

The dorsal longitudinal ligament is a very thin translucent membrane and extends over the dorsal surfaces of the vertebral bodies and intervertebral disks, in the floor of the neural canal. Its attachment extends from the axis to the last caudal vertebra. The fibres of the ligament are smooth and glistening and are firmly attached to the intervertebral disks and margins of the vertebral bodies, but they cover the middle of the vertebral bodies very loosely. Like the ventral ligament, it consists of superficial and deep fibres, and these are disposed in a similar manner.

In addition to the above ligaments, there are intervertebral ligaments which connect the margin of one vertebra to that of the next. These ligaments consist of short thin fibres and are placed at the sides between the ventral and dorsal longitudinal ligaments.

OBSERVATIONS ON THE INTERVERTEBRAL JOINTS OF YOUNG ALBINO-RATS, VARYING IN AGE FROM ONE-DAY TO TWO MONTHS

The vertebral and the intervertebral regions of the spinal column in a new-born rat are clearly differntiated. The notochordal remnant is confined to the middle of the intervertebral disk forming the nucleus pulposus; only a small tract of homogeneous acellular mucoid material marks the old site of the notochord. This is seen in the middle of the cartilaginous ends of the vertebral bodies and also in the adjoining fibro-cartilaginous part of the disk, which separates the nucleus from the epiphyseal end of the vertebral body (Figs. 40 and 41). The mucoid streak is obliterated by advancing ossification in the vertebral bodies and concomitant growth of the disk, and is not found to be present after the fourth week.

In a new-born rat, the ossification centres are present in the middle of the vertebral bodies, but the cranial and the caudal ends of each are formed of cartilage (Figs. 41 and 43). With advancing age ossification extends throughout each vertebral body leaving only a thin cartilage plate at the cranial and caudal end. This is well-marked in a 4-week old rat, where each cartilage forms the epiphyseal plate of the vertebral body (Fig. 43). The epiphyseal ends of adjacent bodies are firmly connected together/

together by a fibro-cartilaginous disk. The ossification of each epiphyseal plate proceeds from several centres. It is first noticed in the sacral and caudal regions of the 4-week old rat (Fig. 44), then it extends slowly in the epiphyses of the lumbar, thoracic and cervical regions of the column in succession. In the sacral region of a 4-week rat, the epiphyses of the adjacent vertebral bodies are partially synostosed around a small mass of nucleus pulposus, which lies in the middle of the intervertebral region. The sacral vertebrae undergo complete ankylosis a little after the second month, when the nucleus pulposus degenerates and disappears altogether.

The intervertebral disks, in a new-born rat, are well-defined and present a considerable thickness. Each disk is almost as thick as the length of the vertebrae between which it lies (Figs. 40 and 42). With advancing age the disks get proportionately thinner, forming about one-third to one-fourth of the length of the vertebral bodies. The disks are thicker ventrally than dorsally in the cervical and lumbar regions, but in the thoracic and caudal regions they are thicker dorsally. In the caudal region in a new-born rat, ventral to each intervertebral disk, there is a small cartilaginous nodule in the/

the median plane (Fig. 42), which, in the fifth-week, undergoes ossification and forms the chevron bone. This bone is not found in the last five or six joints towards the tip of the tail. Each chevron bone is connected with the margins of the adjoining vertebral bodies and to the corresponding disk by fibrous ligaments.

Each intervertebral disk consists of two main components, a peripheral fibro-cartilaginous part, the annulus fibrosus, and a central soft gelatinous part, the nucleus pulposus.

The annulus fibrosus, in a new-born rat consists of a thin outer zone of closely aggregated fibres, which run in fairly parallel rows from one vertebra to the next (Figs. 40 and 42). The most superficial part of this zone is represented by young fibrous tissue, which is continuous with the ventral and dorsal longitudinal ligaments and also with the periosteum of the adjacent vertebral bodies. In between the fibres are found young fibroblasts, which, with advancing age, become thin and flat. No fundamental change in this zone is noted during the later period, except for the increasing presence of densely aggregated collagen fibres and their complex and intricate arrangement. Within this area is the inner fibro-cartilaginous/

fibro-cartilaginous zone of the annulus, where the matrix is abundant, and young cartilage cells and fibres run in parallel rows with an outward convexity (Fig. 40); the cells, near the nucleus pulposus, encircle it and also pass to mingle with those of the epiphyseal plate at the ends of the adjacent vertebral bodies (Figs. 40 and 41). Within the epiphyseal plates, into which the fibres of the annulus pass, flattened cartilage cells are observed which are arranged in rows parallel to the articular surface (Figs. 40 and 41). The collagen fibres of the annulus pass across the intervertebral space, with their convexities outwards, and terminate in the matrix of the epiphyseal plates (Fig. 40). With advancing age, the arched fibres are more clearly recognised and the cartilage cells well-formed (Figs. 45 and 46), then the innermost part of this zone shows well-defined fibres and is thickened to form the fibro-cartilage envelope of the nucleus pulposus. In a 4-week old rat, the fibro-cartilaginous zone of the annulus shows considerable growth and forms the major portion of the disk, encroaching upon the nucleus pulposus, both ventrally and dorsally (Fig. 43). This encroachment of the annulus upon the nucleus not only reduces the

latter in size but also makes its outline somewhat irregular. The cartilage cells and collagen fibres in the outer part of the fibro-cartilaginous zone are disposed concentrically (Figs. 45 and 46) but those in the inner part are irregularly arranged and do not show any laminations (Fig. 43). The outer fibres terminate in the matrix of the epiphyseal plates but the inner fibres surround the nucleus pulposus separating it from them. The innermost part of this zone is deeply stained and distinct forming a clear line of demarcation between the annulus and the nucleus pulposus (Fig. 44). From one month onwards, the line of demarcation is gradually lost, due to the mingling of fibres from the innermost zone of fibro-cartilage with the peripheral part of the nucleus pulposus; this is seen both ventrally and dorsally in the median sagittal sections (Figs. 43 and 47).

The nucleus pulposus is a soft, gelatinous mass contained within each intervertebral disk. In a new-born rat, it forms a considerable part extending for about two-thirds the dorso-ventral length of the disk (Figs. 40 and 43). It is a flattened oval, in the median sagittal plane, and is clearly demarcated from the annulus fibrosus by a deeply stained fibro-cartilage envelope (described above/

above). The nucleus pulposus consists of notochordal cells, which are polygonal and vesicular with large deeply stained nuclei. The whole mass of the nucleus is so arranged, that it gives the appearance of a network with the nuclei being disposed at the knots (Figs. 40 and 41). Between the cell spaces, especially towards the periphery, a homogeneous, slightly basophilic, mucoid substance is observed. The nucleus has a tendency to shrink from the surrounding annulus fibrosus, leaving a space between them (Figs. 40, 41 and 42); this space is an artefact, produced during the process of fixation and dehydration of the tissue.

From birth until the end of the fourth week, there is an active proliferation of notochordal cells with very little accumulation of mucoid material. Various degrees of vacuolisation of the notochordal cells are observed leading to the formation of a meshwork of extremely delicate fibres. The nuclei of the cells are scattered in the mesh but the cell outline is lost. After this period there is a progressive, but gradual, reduction of the nucleus pulposus, due to active growth of the fibro-cartilaginous zone of the annulus, both ventrally and dorsally; as a result, the outline of the nucleus becomes irregular/

irregular. From one month until old age there is a progressive invasion of the peripheral part of the nucleus pulposus by fine collagen fibres from the surrounding fibro-cartilaginous zone of the annulus; this has already been described. During this period there is a gradual diminution of the notochordal cells and their nuclei show all stages of senescence. At the same time there is a progressive accumulation of mucoid material in the intercellular spaces. As this process continues, the persisting network of notochordal tissue becomes broken up into isolated clumps of vacuolated cells, scattered through a basophilic gelatinous matrix (Fig. 47). In all the rats, from one-day to two-months old, the nucleus pulposus was situated nearer the dorsal than the ventral part of the disk, in all the regions of the vertebral column.

DISCUSSION

Discussion

General Remarks

The components of the vertebral column and the way in which these structures are formed reflect the habitat in which an animal lives. Thus, great diversity is noticed in the vertebral column, not only in the number and the form of the vertebrae but also in the variety of joints existing in different species and in different regions of the same species. The type of intervertebral joint in a species is independently evolved according to its own inherent pattern of growth.

With the evolution of the vertebral column from the lower to the higher vertebrates, the growth, form, structure and the fate of the notochord are greatly changed. This change, in the intervertebral region, depends upon the type of joint which eventually develops between the bodies of the vertebrae.

Under these circumstances it has been considered advisable to discuss the joints between the bodies of the vertebrae of each species individually and separately.

Fish/

Fish

The vast majority of fish are amongst the aquatic vertebrates, and show little variation throughout the length of the vertebral column; only trunk and caudal regions are distinguished and the line is drawn where the ribs are transformed into haemal arches. Such a column does not have to bear the complicated mechanical stresses of carrying the weight of the body, and its main function is to support and to form a strong foundation for the attachment of the body muscles which propel the animal. The body of the fish is supported equally, in all directions, by the liquid medium in which it lives and the column is exposed to no stresses except those associated with motion.

In cartilaginous fish, the vertebral column consists entirely of cartilage, which may, however, be calcified later to some extent. In Teleostei or bony fish, on the other hand, the primary cartilaginous column is either completely replaced by true bone (Boas, 1896), or may consist partly of bone and partly of cartilage. Hence the vertebral column of Teleostei is less flexible than that of the cartilaginous fish, but more so than the solid/

solid bony column of the higher vertebrates.

A true articulated vertebral column is found in the cartilaginous fish, where the vertebral bodies are firmly held together by fibrous ligaments. In Teleostei, the strong intervertebral ligaments are the principal bond of union between the vertebral bodies; these ligaments are, in the writer's opinion, analogous with the annulus fibrosus of the intervertebral disks in mammals, where however the arrangement of the arched fibres is more complicated, to withstand the additional stresses of compression, tension and torsion forces. The placing of fibrous joints between such a large number of vertebral bodies permits considerable flexibility of the column as a whole, through the limited movement permitted at the contiguous surfaces of each joint individually. The presence of tough fibro-gelatinous pads between the amphicoelous bodies is an arrangement which also resists any undue compression between the bodies of the adjacent vertebrae, without affecting the flexibility of the column at the same time. The ventral and dorsal longitudinal ligaments, running along the whole length of the column, hold the vertebral bodies firmly enough to prevent flexion and extension, respectively, at/

at the joints of the column.

The rod-like last caudal vertebra, the urostyle, not only surrounds and protects the caudal portion of the notochord but also forms a rigid support for the tail. According to MacBride (1932), the urostyle represents at least three vertebrae fused together.

The notochord perists in fish throughout the length of the vertebral column and extends caudally beyond the tail end of the column, unlike the notochord in higher vertebrates. It is always invested by two sheaths, and, in Teleostei, the sheaths persist throughout life. The sheaths are especially thickened in the intervertebral regions, where they strengthen the joints. The dilated intervertebral portion of the notochord in fish may be compared only with that of mammals, where also the vertebrae are separated for some time by a remnant of notochord, until the nucleus pulposus is formed in its substance. MacBride (1932) considers that this primitive feature of teleostean fish, being retained in mammals, shows that the latter must have diverged early from the other Amniota. My own observations have led me to conclude that the growth, form and fate of the notochord in any one class of the vertebrate group is characteristic of that class/

class only. Vacuolisation of the notochordal cells is a very characteristic feature; this change is marked in the central area but, towards the periphery of the inter-vertebral region, a nucleated epithelial layer persists to form the chordal epithelium. The persistence of the notochord and its flexible character in fish indicate a primitive grade of vertebral evolution (Young, 1950). Thus it may be postulated that the greater flexibility, so necessary in the vertebral column of Fish, is imparted to it by the persistent notochord.

Considering the observations already made and the functions described above, the joints between the bodies of the vertebrae in Teleostei may be considered as special fibrous joints.

Amphibia

The entire construction of the vertebral column in Amphibia is based on its adaptation to land life. The column is highly specialised to meet the demand of the stress and strain of weight bearing. This is first shown by the completely ossified vertebrae. Secondly, shortening of the column with a fewer vertebrae, especially marked/

marked in Anura, is a characteristic feature of Amphibia as a whole among the vertebrates. Gadow (1909) has pointed out that this shortening of the column is intimately connected with the mechanism of jumping, throwing the fulcrul attachment forwards as much as possible.

Regional variation in the vertebral column of land animals is another characteristic feature, and this is first encountered in Amphibia. In Anura four regions of the vertebral column can easily be recognised namely cervical, trunk (or thoraco-lumbar), sacral and caudal. The form of the vertebrae varies greatly and is, according to Gadow (1909), determined by the mechanical problem of motion. Thus, in the frog, the first and only cervical vertebra is so modified as to support the head. By virtue of the synovial joints between the remaining vertebral bodies, the whole column is adapted to allow flexion and extension in place of the free lateral movement that is characteristic of fish. It would appear that a free movement of flexion and extension might occur in the joints between the adjacent vertebral bodies, but, in fact, the movements are restricted, as contiguous bodies are firmly connected together by strong capsular and lateral intervertebral ligaments. It would not be out/

out of place to mention that no reference has been found to the lateral intervertebral ligaments in the literature. Taking the curvature of the column of the frog in the sitting posture as a basic norm, it has repeatedly been shown that the range of extension exceeds that of flexion and this, in turn, bears comparison with movement in the human vertebral column, where there is also a comparable difference in the extent of movement in the two opposite directions.

The eighth vertebral body is highly amphicoelous and is the smallest of them all. It is connected to the adjoining vertebral bodies by ventral ligaments. As a greater range of movement is possible at the joints between this and the adjacent vertebrae, the central ligaments connecting their bodies impart the additional strength and security so necessary in these joints, for their proper function when jumping. The form and size of the eighth vertebral body allow sufficient leverage for movement in the joints between it and the ninth and seventh vertebrae.

Usually only one sacral vertebra is distinguished in Anura, and this, in frog, supports the hip bones. The double joint between the sacrum and the urostyle allows free movement in a vertical plane only.

The/

The marked reduction of the tail in Anura is another characteristic feature, and thus it is that these tailless Amphibia are specialised as jumpers (Young, 1950). In frogs, with the disappearance of the greater part of the tail, the caudal region of the column is represented by the urostyle, a long unsegmented rod of bone. Gadow (1909) considers that the urostyle is the result of fusion of about 12 or more vertebral rudiments, which, from before backwards, have lost their individuality. It is interesting to note that there is no purpose in articulated vertebrae in the region of the urostyle, because the ilia of the hip bones would prevent flexibility. Gagenbaur (1861) states that this marked shortening of the caudal region of the vertebral column in Anura is the cause of the devolopment of the smaller number of vertebrae.

In Amphibia, except in some genera of Newts (Menobranchis and Amphiuma), the notochord is constricted intervertebrally and dilated intravertebrally, as in Reptiles and Birds but unlike Fish and Mammals. In Anura, the notochord degenerates and disappears early in the intervertebral regions, but it persists in the middle of the vertebral bodies as an isolated vestige. It may be postulated/

postulated, from observations on the young and adult specimens of frog examined, that the central ligaments connecting the adjacent vertebral bodies degenerate and disappear in a cranio-caudal direction, except at the intervertebral joints between the seventh, eighth and ninth vertebrae, where they persist and are necessary to meet the functional demand placed on these joints. No reference has been found to these ligaments in the literature. The central ligaments in Anura may be compared with those of the synovial joints of Birds, which, in the latter, degenerate and disappear completely, long before the adult stage is reached.

The synovial membrane of amphibian joints does not show any elastic fibres, though Davies (1946) remarks that the movable parts of the synovial membrane in the joints of man and ox show an abundance of elastic fibres, but they are sparse where the membrane is intimately attached to the underlying tissue. He further states that the villi are devoid of elastic fibres except in the walls of their blood vessels.

Reptilia

The reptilian vertebral column shows a striking change/

change from the column in fish and amphibia, which have already been discussed, and is akin to the column of birds and mammals as five distinct regions can be identified in it, namely cervical, thoracic, lumbar, sacral and caudal; it is in reptiles that the lumbar region is first identified. This regional division, already discussed in relation to the amphibia, is a characteristic feature of land animals. The completely ossified and elongated vertebral bodies are procoelous in Lacertilia, though they may vary in their form in other reptilian groups.

From the observations made on the vertebral column of the adult Lacerta viridis, it is evident that a more generalised type of secondary cartilaginous joint exists between the vertebral bodies than elsewhere within the reptilian class. The modifications of these joints in other Reptiles have produced a specialised condition, which is in contrast to the more generalised structure represented by the Lacertilia. Thus it may be postulated, that the generalised type of joint, as found in Lizards, is a more primitive one.

The devlopment of intervertebral fibro-cartilaginous disks between the bodies of the vertebrae is another important feature of land animals (Rockwell, Evans and Pheasant/

Pheasant, 1938). The reptilian disks may be compared in many respects with those of the mammals, although they are relatively smaller, almost entirely fibrous, and without the characteristic nucleus pulposus of the mammalian disks. The disks are relatively thin and only a small amount of movement is possible between the adjacent vertebral bodies. The solid fibrous nature of the disk in Lacertilia is very characteristic of these animals. This type of articulation between the vertebral bodies, on account of the multiple segments in the column, allows considerable flexibility without diminishing its strength. Dorso-ventral movement is quite restricted in the joints of Lacertilia but considerable lateral flexion is permitted. Both dorso-ventral movement and rotation at the inter-vertebral joints are powerfully checked, not only by the disks but also by the articulations between the neural arches. Extension is limited by the prominent, dorsal margin of the concave surface of the body and also by the strong, ventral longitudinal ligament.

The intervertebral disks, although always relatively thin, vary in thickness in different regions of the vertebral column, which allow varying degrees of flexibility in the different regions of the column. The disks are thickest/

thickest in the caudal region, where the column is most flexible, and thinnest in the sacral region.

A distinct well-developed cervical region, characterised by a diminution in the costal elements of these vertebrae, allows this part of the column to have a mobility that permits the head to be carried free of the ground. The character of the cervical vertebrae, caudal to the second, allows some lateral movement at these vertebral joints in addition to the greater amount of movement that is permitted between skull and column, and atlas and axis. The presence of the wedge-shaped haemapophyses, on the ventral aspect of the intervertebral joints in the cervical region, tends to strengthen and stabilise these joints, that carry the weight of the head (Owen 1866).

The two vertebrae, which together form the sacrum, are not fused and each vertebral body is very short. The opposing surfaces are relatively flat and are connected together by a thin intervertebral disk, which ensures adequate stability in this region.

The caudal region of Lacertilia is characterised by its greater length and the presence of chevron bones in the intervertebral regions. Williston (1925) has remarked that "The length of the tail depends so much upon habit, that/

that it may be extremely variable even in members of the same order. As a rule, the swift moving, crawling reptiles have a long slender tail, while short-tailed reptiles are invariably slow in their movements upon land". The chevrons, in addition to providing strength at the inter-vertebral joints and protecting the caudal blood vessels, furnish greater attachment and better leverage for certain tail muscles enabling them to act more effectively on these joints. The significance of simple rod-like vertebrae in the caudal region lies in allowing free movement of the tail. The chevrons articulate, as a rule, intervertebrally (as they always did in Lacertilia, which I examined,) but sometimes exclusively with the caudal part of the preceding vertebral body, with which they may be ossified.

Cope (1888) has given the name intercentrum to the little nodule of bone which is recognisable, usually, only in the intervertebral regions of the neck and the tail. These have been described in this thesis as the haemapophyses in the cervical region, and the chevron bones in the caudal.

Wiedersheim and Parker (1907) have mentioned that the notochord, in Reptiles, remains expanded longer in the intravertebral region that intervertebrally. Gagenbaur (1878) has noticed a constriction of the notochord between the/

the vertebrae. Both Wiedersheim and Parker, and Gagenbaur have claimed that the notochord disappears completely and is replaced by bony tissue. Gadow (1933) has pointed out that the last traces of the notochord vanish during adolescence. The adult specimens of lizards I have examined show the presence of the notochord as a very small vestigeal remnant at the centre of the inter-vertebral disk. This notochordal remnant may be compared with the much larger nucleus pulposus of the Mammalian intervertebral disk.

In conclusion, according to the writer's opinion, by far the greater part of the intervertebral disk in Lacertilia may be considered homologous with the annulus fibrosus of the mammalian disk. The fibre arrangement of the disk in Lacertilia is most irregular and does not show any lamination which, in higher vertebrates, is remarkably characteristic. The fibres of the Lacertilian disk follow the curvature of the disk.

Birds

The Avain vertebral column shows regional variation of vertebrae, a feature which is first encountered in Reptiles/

Reptiles and to which reference has already been made. The synovial joints between the vertebral bodies in the cervical and the thoracic regions of Birds may be considered highly specialised and modified; they are developed according to the need for adaptation to the medium in which the bird lives. Froriep (1883) has expressed that the evolution of the vertebral column in Birds, in general, follows the same plan as in Reptiles. It is on this basis that the Avian column is often likened to that of many Reptiles, but in view of the difference in their environment, there is a reflected difference in the column. Furthermore, Quiring (1950) states that the specialisation of the Avian vertebral column is in many respects analogous with that of the amphibian Anura, where peculiar locomotor habits are correlated with a specialised skeletal axis.

Birds, as a class, are adapted for aerial life and many parts of their organisation are greatly modified, in accordance with the demands of flight and their bipedal locomotion on land. The vertebral column of Birds, in general, shows a number of well-marked characteristics; these contrast strongly with the more general character of the column in the higher vertebrates. The cervical region/

region is exceedingly long, about as long as the remainder of the vertebral column put together, and is remarkable for its extreme mobility. The trunk region, on the other hand, is characterised by extreme rigidity and the marked tendency shown by the component vertebrae to fuse together into one almost continuous mass. The caudal region of the column, however, is remarkable for its shortness.

The vertebrae are strongly ossified and no epiphyses are ever present at the ends of the vertebral bodies. The zones of proliferation and growth, present at the cartilaginous ends of the vertebral bodies of the young chick, are replaced by bone in adult life.

The free vertebrae of the cervical and thoracic regions are heterocoelous or saddle-shaped, at all ages examined after hatching, and those of the caudal region are slightly amphicoelous. Gadow (1933) writes, "the embryonic vertebrae of all Birds are at first amphicoelous, then they change through opisthocoelous into heterocoelous or saddle-shaped type, which is a combination of procoelous and opisthocoelous and represents the highest stage of interaxial joint.....". The saddle-joints between the vertebral bodies in the cervical region allow much freedom

of/

of movement, so that the bird can look directly backwards and the beak can reach the coccygeal oil-glands.

The articular hyaline cartilages, at the ends of the vertebral bodies, show changes which occur with increasing frequency as the age advances. In old age, the cartilages become relatively thinner and the smooth free surface of the cartilage of the young chick is changed into an uneven surface. Fibrillation, a diminution in cellularity, heterogeneous changes in the matrix and the appearance of occasional fissures and clefts are characteristic age changes in the articular cartilages of adult birds over two years. Similar age changes in the articular cartilages of the knee joint in human have already been observed by several workers (Bennett, Waine and Bauer, 1942).

The intervertebral meniscus, between the bodies of the cervical vertebrae, prevents any undue friction between the adjacent articular surfaces. The hyaline nature of the meniscus in young chicks is gradually changed into fibro-cartilage with advancing age. Gadow (1933) states that the intervertebral meniscus of Birds is analogous with the annulus fibrosus of Mammals. Such a view is open to question and is discussed later in this thesis.

The/

The synovial membrane, which consists of areolar type tissue in the young chick, is changed into a definite fibrous type with advancing age. No other marked change occurs in the synovial layer, except the formation of some occasional folds, especially found in the thoracic region. No definite elastic fibres are found in the synovial tissue of the young and adult birds examined, though Davies (1946) describes their occurrence in the synovial membrane of mammals, and reference to this has already been made with the discussion of Amphibia.

The vertebral bodies of the thoracic and the lumbo-sacral regions are distinct in the column of the newly-hatched chick but they become fused soon after hatching. In the column of the adult bird, these vertebral bodies are indistinguishable as separate compponents, due to complete bony ankylosis between them. As in Reptiles, two sacral vertebrae are present, but unlike them, these vertebrae are completely fused; also, a large number of pre- and post-sacral vertebrae are added to these primary sacral vertebrae, to form a secondary sacrum, commonly called the synsacrum, which is connected to the ilium.

In/

In an articulated skeleton of Birds, the caudal region froms the Uropygium, which is composed of a number of free vertebrae and the pygostyle. This is a single unit which in life supports the tail feathers. Gadow (1933) asserts that the pygostyle is formed from six or seven original caudal segments. In the caudal region, the intervertebral disks, between the amphicoelous bodies of the vertebrae, are hyaline in character in young chicks, but with advancing age they become gradually fibro-cartilaginous. The centre of the disk is primarily occupied by the remains of the notochord but later, in adult life, the notochord degenerates and disappears and is replaced by the fibro-cartilage of the disk. Still later, the fibre architecture of the disk is lost as its centre and irregular clefts and fissures appear there. The fibro-cartilaginous zone of the disk in Birds may be compared with the inner zone of the annulus fibrosus of the inter-vertebral disk in Mammals. As there are no free articular surfaces in such a joint in the caudal region, movement depends upon the flexibility of the disks.

The general framework of the bird vertebral column shows three regions where the vertebrae are free and movable/

movable, and three regions in which the vertebrae are fused. These regions are so arranged that a free and movable region alternates with a fused one. The movable regions with free vertebrae include:

1. All the cervical and the first thoracic vertebrae; this part is very freely movable, hence the neck muscles are large and well-developed.
2. A small segment, formed by the sixth thoracic vertebra, where very little noticeable movement is encountered.
3. A short slender region, consisting of five caudal vertebrae (2nd to 6th), which allow considerable movement of the tail; this region, as might be expected, shows fairly well-developed tail muscles. All the caudal vertebrae, except for the first, and the pygostyle are freely movable, thus allowing the tail to be used as a rudder during flight.

The fused regions of the vertebral column include:

1. A rigid segment from the second to the fifth thoracic vertebra, which provides added strength and effective support during flight.
2. A long bony column consisting of the whole of the/

the lumbo-sacral region with the last thoracic and the first caudal vertebrae, which together form the synsacrum. The greater part of the synsacrum participates in the formation of the pelvis and acts like a girder, for the transmission of the body weight to the legs; a small part of the synsacrum at its cranial end forms a central rigid support, which is associated with the muscles concerned with flight.

3. A SMALL segment, formed from the terminal caudal vertebrae, called the pygostyle, which supports the coccygeal oil glands and the tail feathers.

The fusion of the vertebrae, in the above mentioned regions of the Avian vertebral column, limits the number of joints at which movements may occur. Associated with the reduction of movable joints, the axial muscles show a corresponding reduction, especially the dorsal muscles opposite the fused thoracic and lumbo-sacral regions. Thus the whole thoraco-lumbo-sacral region forms a strut, which carries the weight of the trunk and allows only minimal movement between the 5th, 6th and 7th thoracic vertebrae.

Avian Notochord

The segmental curvatures of the notochord have attracted the attention to several workers. Carlier (1890) has observed, in sheep embryos, slight v-shaped bends of the notochord in the region of the future inter-vertebral disks. These curvatures have been described in the embryos of human and lower mammals by Minot (1907), in the human embryos by Sensenig (1949), Peacock (1951) and Walmsley (1953), and in Mus by Dawes (1929). Minot (1907) has stated that the notochord is convex ventrally within the vertebral body and convex dorsally in the intervertebral region. He has maintained that the general character of these curvatures of the notochord is the same in all species of mammals. My own observations on chick embryos show segmental curvatures of the notochord, which are convex ventrally in the intervertebral regions and convex dorsally within the vertebrae; though in older embryos, these curvatures are not so well-marked in the lumbo-sacral and caudal regions of the vertebral column. The writer believes that the segmental curvatures of the notochord are of general occurrence in all/

all species of Birds and Mammals, but the nature of their disposition is different in different species and is characteristic of that species only.

It would not be out of place to mention that, in addition to the segmental curvatures, the notochord possesses regional curvatures. These curvatures are characteristic of each species and are developed according to their own fundamental pattern. Both the segmental and regional curvatures of the notochord are transient and found only in the embryonic period of development.

The moniliform appearance of the notochord in chick embryos has been recognised by Gagenbaur (1862) and Froriep (1883). Williams (1942) has stated that a slight moniliform appearance of the notochord in chick first appears at the 75th hour of incubation and by the 85th hour the intersclerotomic constrictions and intra-sclerotomic dilatations can be clearly seen. Froriep (1883) has mentioned that the first change in form of the notochord appears in the cervical region of the chick at the end of the 5th day of incubation. Gagenbaur (1862), Froriep (1883) and Piiper (1928) have recorded that the notochord is dilated intervertebrally and constricted intravertebrally during the 7th and 8th day of/

of incubation. This condition is also observed in a 10-day chick embryo by the writer. It is interesting to note that in the embryos of 15 days incubation there is a reversion in the disposition of the dilatations and constrictions of the notochord, the former condition being found in the intravertebral regions and the latter in the intervertebral regions. The stage of 3 dilatations and 4 constrictions, which has been described by Gagenbaur (1862), Froriep (1883) and Lillie (1952) in chick embryos from 9th and 10th day onwards and by Piiper (1928) in Larus of 8 days incubation, has been observed and confirmed. This moniliform appearance of the notochord persists during the whole incubation period until the first two days after hatching; whereas in Larus, as Piiper (1928) has stated, the middle dilatation of the notochord, within the vertebral body, is greatly reduced on the 10th day of incubation, and the smaller dilatations at the end are enlarged.

In man and other mammals, the notochord shows dilatations and constrictions, with a definite segmental distribution in each species. Williams (1908) expresses that, in most mammals, there is a slight dilatation of the notochord within each vertebra and this is usually obliterated/

obliterated with the chondrification of the vertebra. He further states that, in the process of intravertebral constriction, the notochordal cells are forced into the intervertebral disk and this view is supported by Dawes (1929). William (1942) asserts, with Piiper (1928), that this variation in the form of the notochord in Birds, is not caused by internal but by external forces and is due to the unequal growth of the different segments of the perichordal tube (or ring). The writer would like to point out that, in chick embryos and in new-born chicks, the chondrification and subsequent ossification of the vertebral bodies replace the degenerating notochord within them without altering the form of the notochord in the intervertebral regions; while similar changes in the mammalian vertebral bodies show a concomitant dilatation of the notochord in the intervertebral regions. This disproves the views of Williams (1908), Piiper (1928) and Dawes (1929). The writer believes that the moniliform differentiation of the notochord does not show the same distribution in the different animals and in the different regions of the column of the same animal, neither does it occur at the same period of development in the different species. Great diversity of form and segmental differentiation/

differentiation render it difficult to determine the normal type of development of the notochord. Thus, the writer has been led to conclude, that the development of the notochord, its enlargements and fate in any one species are remarkably characteristic of that species, according to its own inherent quality of growth.

The cytomorphosis of the notochordal tissue is very characteristic of each species and is different in different species of animals. In chick embryos of 3 days incubation, the notochord is cellular, resembling an epithelium; later it is so vacuolated as to develop a syncytial network containing mucoid substance in its mesh. This is followed by a marked regression of notochordal cells on the 10th day of incubation. This change is segmental in character and is mostly observed in the vertebral regions, whereas in the intervertebral regions, a few isolated notochordal cells persist. After this period the notochord becomes again cellular and eventually vacuolated in the vertebral regions. At this stage the notochordal tissue may resemble cartilage but is not regarded by the writer as typical hyaline cartilage because of the nature of its ground substance and the arrangement of its cells. In the later period

of/

of embryonic life, as well as in the newly-hatched chicks, a characteristic aggregation of notochordal cells occurs in the intervertebral regions. Kölliker (1867) and Williams (1908) state that the appearance of this intervertebral notochordal aggregation is due to their passive displacement from the vertebral bodies. Walmsley (1953) describes a similar localised aggregation of notochordal cells in a 17 mm. human embryo at the level of the developing intervertebral disks. My own observations have led me to believe, with Walmsley (1953), that the aggregation of the notochordal cells in the intervertebral regions is the result of their active proliferation, irrespective of the chondrification of the vertebral bodies. The writer would further like to conclude, in agreement with Walmsley, that the notochord possesses an inherent quality of segmental differentiation which is remarkably characteristic of certain groups of animals.

Mammalia

The vertebral column in Mammals has reached the highest stage of evolution; all the five regions, described in the columns of Reptiles and Birds, are more clearly distinguished in this group, except in whales where the sacral region is absent. Most of the vertebrae remain distinct and free throughout life, and the fully ossified vertebral bodies are usually connected together by fibro-cartilaginous intervertebral disks. The vertebral bodies in mammals differ from those of the sub-mammalian forms in having epiphyses, one at the cranial and one at the caudal end of each body, though they are not found in some Monotremes and in Sirenia. In most quadruped mammals, each epiphysis is a complete discoid plate of bone, which unites with the vertebral body comparatively late; but in humans, the ends of the vertebral bodies are covered with cartilage plates, except at the periphery where a bony epiphyseal ring is found. Schmorl (1928) and Beadle (1931) have attempted, in man, to define the epiphyseal ring and the cartilage plate of the vertebral body as two different structures, though Keys and Compere (1932) have stated that these two have the/

the same genetic origin. The writer agrees with the belief of Keys and Compere (1932) that the complete ossification, which is observed in the epiphyseal plates of mammals, does not extend to the central part of the cartilage plate in man but is confined to the peripheral portion, where it forms an annular bony epiphysis. The cartilage plate and the epiphyseal ring in man, therefore, may be considered homologous with the bony discoid epiphyseal plate of other mammals.

The cranial and caudal ends of the vertebral bodies are usually bi-plannar or amphiplatyan in most mammals, except in some ungulates where, in the cervical region, the vertebral bodies are opisthocoelous and form synovial joints. With a few exceptions, most of the vertebrae in mammals are intimately connected by fibro-cartilaginous disks. These allow for different, but limited, degrees of mobility in different regions of the column. Movement is greatest, of course, in the tail region, which can be bent in any direction; this is due to the presence there of very thick intervertebral disks. Except in the sacral region, where the vertebrae are fused together to form the sacrum, mobility is least in the thoracic region, on account of the thinness of the intervertebral disks and also/

also due to the presence of overlapping neural spines.

The intervertebral disks form the main bond of union between the vertebral bodies. Rockwell, Evans and Pheasant (1938) have reported that, with a few exceptions, the intervertebral disks of most mammals become secondarily fibro-cartilaginous. As the vertebral column of mammals is more exposed to compression, tension and torsion stresses than that of the sub-mammalian forms, the intervertebral disks reach the highest stage of their development. They show a complex and intricate structure, adapted not only to their position in a particular vertebral region but also to the stresses of the forces working upon them.

There is a marked similarity between the basic structure of the human intervertebral disk and its condition as seen in other mammals, where it may also be described as consisting of two main components- an outer, fibro-cartilaginous, annulus fibrosus and an inner, soft, nucleus pulposus. In the human some workers include the cartilage plates, at the ends of the adjoining vertebral bodies, as parts of the disk, while others describe them as parts of the vertebral bodies. In this discussion, the epiphyseal plates are not included as

parts/

parts of the disk, though the two elements are closely associated, not only structurally but also functionally, with each other. No synovial cavity is recognisable within any of the intervertebral disks of the albino rat; however, such cavities have been reported within the human disk, first by Luschka (1858), and later by Schmorl (1928), Geist (1931), Smith (1931) and Frykholm (1951).

The annulus fibrosus of the intervertebral disk in an adult rat presents a narrow outer zone of closely aggregated collagenous fibres and an inner zone of fibro-cartilage. In the young rats, examined, the outer zone of the annulus shows young fibroblasts and very little collagen fibres. With advancing age, this zone becomes densely aggregated with collagen fibres and the cells are reduced to thin plates, where only the nuclei are recognised. The fibres run across the inter-vertebral space, following an outwardly convex course. The laminae have an oblique orientation as they pass between contiguous vertebrae and furthermore, as adjacent laminae run in different directions, the outer part of the annulus has a criss-cross arrangement. Thus it is evident that the direction of fibres in the annulus changes/

changes with the many layers that are present, and, by so doing, the fibres are better able to withstand any rotational stresses, to which they are subjected. The most superficial of these fibres, ventrally and dorsally, blend with the fibres of the longitudinal ligaments. The terminations of the deeper arched fibres are lost in the matrix of the epiphyseal plates of the adjacent vertebral bodies but, in the human, they are embedded in the epiphyseal ring (Peacock, 1952). Carlier (1890) has pointed out that this zone of the annulus in sheep is, from the first, composed of fibrous tissue and this fibrous character is retained throughout life. However, in a rat of 2 years, the fibre architecture is lost in the outer zone and the collagen fibres show hyalinisation which is comparable to the condition described in old people by Peacock (1952).

Within the outer zone of collagen fibres, there lies an inner fibro-cartilaginous zone, and this forms the major part of the annulus. This zone is relatively small in the disks of young rats but later, by proliferation of the cells and growth of the fibres, it forms the major tissue component of the disk. There is no clear line of demarcation between the outer and inner zones of the annulus/

annulus as one merges gradually with the other. The fibre architecture of the inner zone consists mainly of outwardly convex, arched fibres with a few oblique fibres as well. The fibre arrangement described by Carlier (1890), in sheep, is confirmed. The innermost part of the fibro-cartilaginous zone of the annulus, immediately surrounding the nucleus pulposus, stains sharply and is clearly defined. From one month onwards, the fibro-cartilaginous part of the annulus fibrosus increases in extent, growing inwards towards the nucleus pulposus. The laminated arrangement of the fibres and cells is preserved outwardly but in the innermost part the arrangement is irregular, the cells are fewer in number and the laminar appearance is absent. As seen in sagittal sections, the growing fibro-cartilage encroaches ventrally and dorsally upon the area of the nucleus pulposus, not only reducing it in size but also making its outline irregular. In these locations, a few fine fibres from the innermost zone of fibro-cartilage may be traced into the peripheral part of the nucleus pulposus. With advancing age, these fibre strands become more numerous; as a result, the clear line of demarcation between the annulus and nucleus, found in young rats

before the age of one month, is gradually lost.

Considerable controversy has existed among early workers (Virchow, 1857; Luschka, 1858; Robin, 1868; Dursy, 1869; Gagenbaur, 1878; Löwe, 1879) concerning the formation of the nucleus pulposus. It is generally believed that it arises by liquifaction of tissues of the disk, and that the notochord may or may not take part in this formation. Williams (1908) has stated that the notochordal cells, in pig, lose their cellular character, become vacuolated and are filled with a mucinous substance; later, they come to resemble cartilage, and persist as nucleus pulposus. Keys and Compere (1932), on the other hand, describe that, in man, the nucleus pulposus is formed by the growth of the fibro-cartilage in the substance of the degenerated notochordal tissue, and this view is supported by Peacock (1951 & 1952) and by Walmsley (1953).

In the rat, the nucleus pulposus is a very distinct and separate structure. There is a sharp line of demarcation between it and the surrounding annulus, until the age of one month; this confirms the results of Williams (1908) in pigs, and Dawes (1929) in Mus. The nucleus pulposus has a tendency to shrink from the surrounding/

surrounding fibro-cartilaginous capsule, developing a space between them; this space is considered as an artefact, which occurs during the process of fixation and dehydration of the tissues. The nucleus pulposus is a soft, pulpy ovoid mass, which normally never disappears but persists in the middle of the disk throughout life. It is nearer the dorsal than the ventral part of the disk in all regions of the specimens examined. In the young rat, the nucleus appears as a flattened, oval mass on sagittal section and occupies more than two-thirds the dorso-ventral diameter of the disk. With the advancement of age, the nucleus pulposus is reduced in size and comes to occupy a small area of the disk, a little dorsal to the central axis of the column. This has already been referred to. In a new-born rat, the nucleus pulposus consists of vacuolated notochordal cells with deeply stained nuclei, arranged in the form of a network; there is very little mucoid material in the intercellular spaces. Until the age of four weeks, the nucleus pulposus enlarges and expands due to the proliferation of its cells and their subsequent vacuolisation. At four weeks this growth falls in abeyance, and from then onwards, until adult life, the notochordal/

notochordal cells slowly diminish in number and undergo gradual senescence. During this degenerative process, the mucoid content is increased forming scattered globules throughout the notochordal tissue, while the network of cells becomes fragmented into irregular strands and isolated clumps. The writer feels quite certain that up to one month after birth, at least, the notochordal tissue forms the main component of the nucleus pulposus. After the age of one month, the substance of the nucleus pulposus is augmented at its periphery by fibres from the innermost fibro-cartilaginous zone of the annulus, to an ever increasing extent. This is shown both ventrally and dorsally, on median sagittal section, where the clear line of demarcation between the nucleus and the annulus fibrosus is lost. Very little difference is noticed in the structure of the nucleus pulposus, as it has been described above, after the age of six months (adult); no cartilage cells have been found in the substance of the rat nucleus pulposus, at any age examined during this investigation. The writer considers that, in lower mammals, the nucleus pulposus remains distinct from the annulus fibrosus throughout life, and that the notochordal cells are always present in it, although they undergo slow and/

and gradual degeneration. The structure of the component parts of the intervertebral disk in the young rat may be compared with the condition present in a new-born child. The most striking feature, common to both, is the clear line of demarcation between the annulus fibrosus and the nucleus pulposus. The fibro-cartilaginous envelope surrounding the nucleus pulposus, both in human and rat, shows an invagination of its fibres in the substance of the nucleus. In man, as opposed to rat, this forms the origin of the fibrous tissue found in the adult nucleus pulposus (Robin, 1868; Keys and Compere, 1932; Peacock, 1951; Walmsley, 1953); in rat, fibres only are found in the peripheral part of the nucleus. As a child grows older, there is a progressive replacement of the notochordal cells in the human intervertebral disk by collagen fibres and cartilage cells, so that ultimately the nucleus pulposus may be transformed completely into fibro-cartilage. Although the notochordal cells in rat do undergo senescence, this change is gradual and does not involve all the cells at any time; hence notochordal cells, in varying stages of degeneration, are always found in the nucleus pulposus throughout life. Peacock (1951) and Walmsley (1953) have said that the line of demarcation between the annulus and the nucleus, in/

in the human, is broken by a process of liquefaction of the innermost part of the fibro-cartilaginous zone. Walmsley states clearly that this results directly from the action of the notochordal cells.

The homology of the intervertebral disk or meniscus is still a subject of controversy. Developmentally, the intervertebral regions of the adult animals are not quite homologous in all species of the vertebrate group, as each is highly modified and specialised and has diverged greatly from the original structure. Gadow (1933) has pointed out: "that 'intervertebral' is a relative expression which does not imply homology". He has quoted Gagenbaur (1898): "The separation of the continuous Anlage into the vertebral bodies is effected in Lizards and Snakes by the division of the intervertebral cartilage into a posterior knob and an anterior cup, by which feature these creatures are connected with the Amphibia. In Crocodiles and Birds these cartilages between the centra are turned into a special apparatus: either it remains as such (Crocodiles), or it forms inter-cartilage, menisci, which are separated from the centra by joint cavities (Birds)". Gadow (1933) has again stated/

stated "If the chorda is destroyed intervertebrally, this is done by the big knob formed by the pronounced procoelous or opisthocoelous vertebrae. Even the amphicoelous can change into the procoelous or opisthocoelous condition by the knob formed by the centrum, which stamps a hole into the meniscus and converts it from a disk into a ring; there is no room left for the nucleus pulposus".

The writer's own interpretations, on the comparative study of the intervertebral joints in different vertebrates, are based on the adult specimens examined (Fig. 48). The mammalian intervertebral disk may be compared with that of Fish and Reptiles, and with the meniscus (intervertebral) of Birds. The annulus fibrosus of the mammalian disk has been considered analogous with the intervertebral ligament of Fish and homologous with the greater part of the intervertebral disk of Reptiles. Under conditions of compression, tension and torsion forces, the simple arched fibres of the intervertebral ligament in primitive fish have become highly modified and specialised, in adaptation to the changing environment; the result is the complicated and intricate fibre arrangement of the annulus fibrosus of the mammalian disk. The corresponding component in Reptiles and Birds is again highly modified to form, respectively, the fibro-cartilaginous disk and the intervertebral/

intervertebral menisci. These structures have developed according to the respective functional demands of the particular environment, in which the animals live. The capsular ligament of the intervertebral joint of the amphibian Anura may be compared and considered analogous with the annulus fibrosus of the mammalian disk. Beadle (1931) considered that the annulus fibrosus may be compared with the fibrous capsule of any normal synovial joint.

The notochord, in Fish, persists throughout the length of the vertebral column; in Teleostei, it is dilated at the intervertebral region and constricted within the vertebral body (Fig. 48). In Lepidosteus, on the other hand, where the vertebrae are opisthocoelous, the notochord is highly constricted in the intervertebral region (Goodrich, 1930). In Mammals and, of the Reptiles, in Lizards, Geckos and Sphenodon the notochord persists longer in the intervertebral regions than in the vertebral regions. In the adult Lizard, which I have examined, the vestigeal remnant of notochord within the intervertebral disk may obviously be compared with the nucleus pulposus of the mammalian disk and also with the intervertebral notochordal dilatation in bony Fish (Fig. 48). But, in Birds, and most other Reptiles, the notochord disappears completely/

completely. The same is true of the notochord in Amphibia except for a small remnant, which always persists within the vertebral body.

SUMMARY

Summary

1. A comparative study of the joints between the vertebral bodies in different vertebrate animals has been made.

2. The nature of the intervertebral joint in different vertebrate groups is dependent on its inherent pattern of self-differentiation.

3. In Elasmobranchs the cartilaginous composition of the vertebrae contributes to the flexibility of the column, but the notochord remains as a well-defined structure throughout life, as it does also in the vertebral column of Teleostei.

In Fish, special fibrous joints between the amphicoelous vertebrae allow an effective side to side movement, and the persisting notochord imparts an additional flexibility to the column.

4. Regional variation of the vertebral column is a characteristic feature of land animals; it is first encountered in Amphibia and is greatest in Mammals.

5. In Anura, shortening of the vertebral column, associated/

associated with absence of a tail, is a characteristic feature correlated with the jumping gait. In them, synovial ball and socket joints between the procoelous vertebrae are described, and an account is given of lateral intervertebral and central ligaments, to which there is no reference in the literature. The central ligaments degenerate cranio-caudally with advance in age, except where functional demand requires their persistence at the joints of the amphicoelous eighth vertebra of the frog. Degenerated vestiges of notochord are present within the vertebrae throughout life, and in the central ligaments as long as they persist.

6. Fibro-cartilaginous disks are a feature of many intervertebral joints of land animals and are first encountered between the procoelous vertebrae of Lizards. In them the solid fibrous, non-laminated nature of the disk is remarkably characteristic. The vestigeal remnant of notochord in the middle of the disk of Lacertilia is a noteworthy feature. The major part of the disk is considered homologous with the annulus fibrosus/

fibrosus of the Mammalian disk.

7. In Birds, a description has been given of the synovial saddle joints between the free vertebrae of the cervical and thoracic regions. The articular cartilage, in fowls of over two years, is characterised by a heterogeneous matrix, fibrillation and a diminution in cellularity with occasional fissures and clefts. The central ligaments of the synovial joints degenerate and disappear within ten days of hatching. Secondary cartilaginous joints in the caudal region are described; in them the notochord degenerates and is replaced by an extension from the surrounding fibro-cartilage of the disk.

The functional significance of alternating regions of free and fused vertebrae has been discussed.

The moniliform appearance and the curvatures of the notochord are peculiar to each animal species, at different periods of growth, and this has been discussed following observations on pre- and post-hatched chicks. The notochord possesses and inherent quality of local cell aggregation in the intervertebral/

intervertebral regions resulting in segmental self-differentiation.

8. In Mammals, the annulus fibrosus and the nucleus pulposus of the intervertebral disk remain distinct for a short time after birth; later, the line of demarcation between them is lost. The fibre-architecture of the annulus fibrosus in the Rat shows a basic pattern, characterised by an intricate laminated fibre-system. Initially, the nucleus pulposus is formed by an intervertebral aggregation of notochordal cells, which later undergo gradual senescence; a progressive invasion of fibres occurs from the fibro-cartilaginous zone of the annulus into the peripheral part of the degenerating notochordal tissue.

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